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THE PTEROBRANCHIA OF THE SIBOGA-EXPEDITION

WITH AN ACCOUNT OF OTHER SPECIES

BY

SIDNEY F. HARMER, Sc.D., F.R.S.
Fellow of King's College, Cambridge, and Superintendent of the University Museum of Zoology

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With 14 plates and 2 text-figures

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I. INTRODUCTION AND HISTORICAL.

Among the organisms obtained during the voyage of H. M. S. "Challenger" in 1873—1876, one of the most striking novelties was the animal described by M'INTOSH (**82**) as *Cephalodiscus dodecalophus*. It was trawled at Station 311, in the Straits of Magellan, at a depth of 245 fathoms, from a bottom consisting of blue mud. The gelatinous tube, or coenoecium, contained large numbers of female individuals, and many free eggs; but no trace of a male was to be found. The affinities of the organism were entirely problematical. It was at first thought that it might be a Compound Ascidian, while it was sent to Professor W. C. M'INTOSH for examination on the supposition that it was perhaps related to the Annelids. M'INTOSH, with ALLMAN and BUSK, arrived at the conclusion that its nearest affinities were with *Rhabdopleura*, a result which has been amply confirmed by the subsequent work which has done on the two genera.

Cephalodiscus was introduced to science at the meeting of the British Association in 1882, although the Report of that meeting containing the original description (M'INTOSH, **83**) did not appear until the following year, and was thus preceded by the fuller "Preliminary Note", published by Professor M'INTOSH in the "Annals and Magazine of Natural History" (**82**). There was at this time a general consensus of opinion that *Rhabdopleura* belonged to the Polyzoa, although constituting an aberrant type; and there was at first no reason for suspecting that this genus and *Cephalodiscus* had affinities in a widely different direction. The preliminary notes gave an account of the coenoecium and of its contents, the "polypides", the free ova and the buds.

The general structure of the polypides or zooids was, in many respects, accurately described, particularly so far as concerned the external characters, the alimentary canal and the ovaries. The selection of the specific name, *dodecalophus*, in allusion to the existence of six pairs of tentaculiferous arms, proves to have been fortunate, since the examination of the "Siboga" material shews that the number of the arms is an important specific character. The description of the remarkable pigmented oviducts as eyes is a mistake which is a natural one to have made, in consequence of the eye-like appearance presented by these bodies in an external view of the zooid.

The article "Polyzoa" written by Professor E. RAY LANKESTER for the "Encyclopaedia Britannica" (**85**) contains the first figures which were published of *Cephalodiscus*, these being taken from original drawings supplied by Professor M'INTOSH. The position of *Rhabdopleura* and *Cephalodiscus* as a Section of the Polyzoa is here definitely formulated.

M'INTOSH published his "Challenger Report" in 1887, and at the end of that Report appeared an Appendix in which I was able to demonstrate the close affinity of *Cephalodiscus* to Balanoglossus [1]). This view was disputed by EHLERS in 1890 (p. 164), while in the same year LANG provisionally accepted it in a paper (**90**) written to shew that the differences between *Cephalodiscus* and Balanoglossus were in the main due to the fact that *Cephalodiscus* has taken on a sessile and tubicolous form of life, resulting in the forward migration of the anus and in other departures from the arrangement of the organs found in Enteropneusta.

At the close of his great Monograph on the Enteropneusta of the Gulf of Naples, SPENGEL (**93**, p. 753), as the result or his own investigation, expresses his concurrence with the view that *Cephalodiscus* is related to Balanoglossus.

In 1896—1899 appeared a series of papers by MASTERMAN, who in several important respects extended our knowledge of the structure of *Cephalodiscus*. MASTERMAN was the first to describe the vascular system and the details of the budding processes, while he added considerably to what was known of the nervous system. I shall have occasion to discuss MASTERMAN's results in the later portions of this Report. I ventured to criticize some of them in a note published in 1897, in which year SPENGEL (**97**) also published a few remarks on the same subject.

In 1899 appeared a paper by COLE on the terminal swellings of the tentaculiferous arms of *Cephalodiscus*. These, which had been regarded by MASTERMAN as compound eyes, were described by COLE as having a structure similar to that of the rhabdite-cells of Planarians.

In 1903 MASTERMAN published a further paper on *Cephalodiscus*, dealing with the structure of the "central complex", or region of the proboscis-stalk and adjacent parts.

The whole of the literature mentioned so far was based on the examination of the original "Challenger" material; that is to say, on female specimens of *C. dodecalophus*.

In 1903 ANDERSSON announced the discovery, by the Swedish Antarctic Expedition, of specimens of *Cephalodiscus*, in four dredgings taken in the neighbourhood of the Falkland Islands. The depths ranged from 80 to 235 M. In the absence of a fuller account of the discovery, it

1) I here use this name in its older sense as including all the species of Enteropneusta, now arranged in a series of genera by SPENGEL (01).

may be presumed that the species is probably *C. dodecalophus*. Nothing is said about males, but ANDERSSON was the first to describe the free larvae, which are ciliated planula-like organisms.

In the same year (1903) I published a note announcing the fact that I had in my hands *Cephalodiscus* from Oriental Seas; and in the following year (**04**, p. 26) I mentioned the peculiarities of the remarkable male zooids found in one of these colonies.

In addition to the papers noticed above frequent references to *Cephalodiscus* have appeared in other places. Some of these are discussed in the later parts of this Report; but special mention must be made here of the work of FOWLER (**92**, 1,2), who was the first to demonstrate that *Rhabdopleura*, like *Cephalodiscus*, conforms to the Balanoglossus-type of structure.

II. SPECIMENS EXAMINED.

The material on which this Report is based consists of the following specimens:

(I) A fragment of the original female colony of *C. dodecalophus*, dredged by the „Challenger" in the Straits of Magellan at a depth of 245 fathoms (= 448 M.).

(II). *C. gracilis* n. sp.

"Siboga". Stat. 89. Pulu Kaniungan ketjil, reef. [E. coast of Borneo]. 1 Ex., ♀.

(III). *C. sibogae* n. sp.

"Siboga". Stat. 204. Between islands of Wowoni and Buton; Northern entrance of Buton Strait, 75—94 Metres. Sand with dead shells. [Off S. E. point of Celebes]. 1 Ex., ♂ [1].

(IV). *C. levinseni* n. sp.

A specimen received from the Copenhagen Museum. Obtained in Long. 128° 20′ E. Lat. 32° 10′ N. [Off W. coast of Japan, at the S. end of the Corea Strait], 100 fathoms (= 183 M.). 1 Ex., ♀.

(V). *Rhabdopleura* sp.

"Siboga". Stat. 204. Between islands of Wowoni and Buton, 75—94 Metres. 1 Ex. [This specimen, found during the correction of the proof-sheets, will be described in Section XIX].

The specimen which I propose to call *C. gracilis* was found during the examination of a colony of *Tubucellaria* sp. [2]), one of the Polyzoa which had been entrusted to me for description. It consists of a small number of delicate, almost colourless tubes (coenoecium), whose association with the *Tubucellaria* is probably accidental. The tubes have a prostrate habit, and are supported along the greater part of their length by the calcareous branches of the Polyzoon. Their appearance, as seen with the naked eye (Pl. I, fig. 1) is very different from that of any

1) A fragment of coenoecium, without zooids, has more recently been found by Professor WEBER in material from Stat. 204. It may be part of the male colony described in this Report.

2) The species is probably *T. fusiformis* D'Orb.

of the other species. They are far less conspicuous, and might easily be passed over by any one who was not acquainted with the genus. It is probable that this species will hereafter be found on other marine objects collected during the Expedition. The tubes contain large numbers of the zooids, in a good state of preservation, together with buds and embryos. All the zooids are female. It is specially noteworthy that this specimen was collected between tide-marks, *Cephalodiscus* having previously been regarded as an abyssal animal.

C. sibogae n. sp., (Pl. I, fig. 2) is also represented by a single specimen, which was growing on a small rock. It is a more conspicuous object than the last species; and it had been placed in a bottle by itself and sent to me as a Polyzoon. Although the zooids are unfortunately not well preserved, their state was sufficiently good to enable me to make out some interesting facts with regard to the males, and in particular to demonstrate the occurrence, in *Cephalodiscus*, of an extraordinary sexual dimorphism. The male individuals (Pl. VII, figs. 72—76) are entirely unlike the females found in other species, being without tentacles and possessing only a vestigial alimentary canal. They are accompanied by neuter individuals (Pl. I, fig. 3), which, except in possessing no reproductive organs, have the typical *Cephalodiscus*-structure. These neuters probably perform the functions of digestion and nutrition for the entire colony. No females are present, and the possibility is not excluded that *C. sibogae* is the male form of *C. gracilis*.

C. levinseni n. sp. This species (Pl. I, fig. 10), the property of the Copenhagen Museum, was most generously placed in my hands for description by Dr. G. M. R. Levinsen. On first finding *Cephalodiscus* among the "Siboga" material, I wrote to Dr. Levinsen, to enquire whether he was working at a specimen belonging to this genus which, as I had been informed a year or two previously, was in his possession. It appeared to me not improbable that it might belong to the same species as one of the "Siboga" forms. With the utmost generosity, for which I desire here to express my most cordial acknowledgment, Dr. Levinsen replied by sending me the specimen, and asking me to investigate it with the other material in my hands. It is in many respects a very remarkable species, differing in the clearest way from all the others. The zooids are all female, and numerous embryos are present.

The British Museum have recently received other specimens of *Cephalodiscus*, of which descriptions will doubtless be published in due course.

III. DIAGNOSES OF SPECIES OF CEPHALODISCUS.

The most useful specific characters of the genus *Cephalodiscus* appear to me to be afforded by the coenoecium, the proportions of the body and stalk of the zooids, the number of tentaculiferous arms, and the presence or absence of vesicle-bearing end-bulbs on the arms. The species which have come under my notice can readily be discriminated by these features, but in the short diagnoses which follow I have made some use of other characters, such as the profusion with which buds are produced. Since the diagnosis depends, in each case, upon

a single colony, too much stress cannot be laid upon the buds, the number of which may depend on the season of the year or on the condition of sexual maturity of the zooids.

The descriptions of *C. dodecalophus* which have previously been published were drawn up in the absence of all information relating to other species of the genus; and until this information was forthcoming it was of course impossible to decide which of the characters were of specific rather than of generic value. It may, however, be remarked that the specific name given by M'Intosh proves to have been well chosen; since, as I believe, the number of arms is a character of specific value.

The systematic position which *Cephalodiscus* and *Rhabdopleura* appear to occupy is indicated by the following classification.

HEMICHORDATA [1]).

Bateson (Quart. J. Micr. Sci. XXV, Suppl., 1885, p. 111).

Order 1. ENTEROPNEUSTA Gegenbaur.

Order 2. PTEROBRANCHIA Lankester.
(Quart. J. Micr. Sci. XVII, 1877, p. 448).

= ASPIDOPHORA Allman.
(J. Linn. Soc. Zool. XIV, 1879, pp. 490 n., 586).

= BRACHYSCOLECIDA BRANCHIATA Ehlers (**90**, p. 173).

= CEPHALODISCIDA + RHABDOPLEURIDA Fowler (**92**, 2).

Fam. 1. Cephalodiscidae.

= Enteropneusta Monobranchiata Schimkéwitsch (**93**, p. 238).

Cephalodiscus M'Intosh (82).

Fam. 2. Rhabdopleuridae.

Rhabdopleura Allman.
(Quart. J. Micr. Sci., IX, 1869, p. 57; Rep. Brit. Ass. (1868) 1869, p. 311).

?Order 3. PHORONIDEA.

Phoronis Str. Wright.

1) Numerous other names, such as Pharyngopneusta, Archicoelomata, Trimetamera, Archichorda, Diplochorda, Protochordata, Adelochordata, "Urchordaten", "Axobranches", "Vermidiens", "Procordés", Branchiotrema, Hydrotrema, have been used as the equivalent of Hemichordata, or of this group in addition to others, or of its subdivisions. These terms are for the most part dealt with historically by de Selys Longchamps (04, pp. 102 f.). Reference may also be made to Delage and Hérouard (97, 98) and to Willey (99).

Fam. Cephalodiscidae.

Cephalodiscus M'Intosh.

Zooids secreting a gelatinous coenoecium formed of numerous lamellae. Coenoecium with a continuous cavity or with a separate cavity for each zooid, each orifice produced into one or more peristomial processes. Zooids consisting of proboscis, collar, and metasome. Proboscis greatly flattened in an antero-posterior direction, its anterior wall mainly composed of a high, glandular epidermis, and provided with a curved, transverse pigment-band, with dorsal concavity. Body-cavity of proboscis single, opening to the exterior by two symmetrically disposed proboscis-pores, which lie on either side of a median pericardium. Collar with an anterior free edge, the dorsal part of which is split up to form 4—6 pairs of tentaculiferous arms, between the bases of which is the central nervous system; while the ventral part forms a simple lower lip, operculum, or post-oral lamella. Body-cavity of collar paired, with complete dorsal mesentery, which supports a pharyngeal outgrowth ("notochord") passing forwards along the septum between the proboscis-cavity and the collar-cavities. These open to the exterior by a pair of collar-canals, immediately behind which is a pair of gill-slits situated in the septum between the collar-cavities and the metasomatic cavities. Metasome, body or trunk elongated at right angles to the antero-posterior axis of the zooid, containing the gonads and nearly the whole of the alimentary canal. Anus and generative apertures situated dorsally on the metasome, which is produced ventrally into a muscular stalk, from the distal end of which originate buds. Body-cavity of metasome paired, with complete or incomplete dorsal and ventral mesenteries. Sexes dimorphic.

It will be seen that the generic diagnosis, as above given, includes all the most important features which have previously been described in *C. dodecalophus*. The specific characters are in fact subordinated to the striking assemblage of anatomical peculiarities which have already been recognized in the type-species. The curiously reduced males of *C. sibogae* have not, however, been shewn to possess proboscis-pores, gill-slits or operculum, while the arms are reduced to a single pair, and bear no tentacles.

C. dodecalophus M'Intosh. (Pl. II, fig. 21. Pl. IV, fig. 42, etc.).

C. dodecalophus M'Intosh (82, 83, 87), Lankester (85), Lang (90), Spengel (93, pp. 721, 753). Masterman (97, 98, 03), Cole (99).

Straits of Magellan. "Challenger" Collection. 448 M.

Female colony.

Coenoecium large, reaching a length of at least 225 mm., its cavity continuous, opening at intervals by irregularly arranged orifices, which may bear two or more long peristomial processes. Metasome ovoid [1]), giving off the stalk from its anterior surface. Stalk thick, short

1) The material was, in all the species, preserved without special precautions being taken to obtain the zooids in an extended condition. There is clear evidence, in most cases, that the greater number are in a highly contracted state, and it is this condition to which the diagnoses refer.

(not so long as the rest of the zooid in the contracted condition), and commonly directed towards the mouth, producing buds in small numbers from its free extremity. Tentaculiferous arms six pairs, terminating in end-bulbs, which bear numerous vesicles in their epidermis.

C. levinseni n. sp. (Pl. I, figs. 10, 6, 5. Pl. II. figs. 11—13. Pl. III, figs. 23, 24. Pl. IV, figs. 33, 34, etc.).

Sea between Japan and Corea. 183 M. (Copenhagen Museum).

Female colony.

Coenoecium large, subcylindrical, and slightly branched, reaching a length of at least 132 mm.; consisting of a number of distinct zooecia, the cavities of which do not communicate with one another. Orifices borne at the ends of distinct tubular peristomes, which radiate in all directions, at an angle greater than a right angle, from the principal axis of the branch; each being produced on its abaxial side into a single, short, blunt process which is rarely branched. Metasome elongated and cylindrical, giving off the stalk from its anterior surface. Stalk thick, about as long as the rest of the zooid, usually directed aborally in the adults, producing buds in small numbers. Proboscis-stalk very long, giving rise to a great mobility of the proboscis, which usually forms a mantle-like investment passing partially round the bases of the arms, and is commonly found in an inverted or otherwise displaced position. Tentaculiferous arms six pairs, without definite end-bulbs or vesicles.

I have great pleasure in dedicating this species to Dr. G. M. R. Levinsen, as some slight acknowledgment of the kindness with which he placed the specimen in my hands for description.

C. gracilis n. sp. (Pl. I, figs. 1, 4, 7. Pl. II, figs. 15, 16. Pl. III, fig. 22. Pl. IV, fig. 37, etc.).

"Siboga" Expedition. Stat. 89. E. coast of Borneo, reef.

Female colony.

Coenoecium very small and delicate, with continuous cavity, creeping over other objects, several times branched, and fimbriated at its extremities by long peristomial filaments borne on the margins of the funnel-shaped orifices. Metasome an elongated ovoid, giving off the stalk from its anterior surface. Stalk thin, much longer than the rest of the zooid, usually directed aborally, and producing buds in great profusion. Tentaculiferous arms five pairs. Small end-bulbs, bearing visicles, present in the first two arms of the bud, and occasionally in the third arms; apparently absent in some of the adult specimens.

C. sibogae n. sp. (Pl. I, figs. 2, 3. Pl. II, figs. 17, 18. Pl. IV, figs. 38, 40. Pl. VII, figs. 72—76, etc.).

"Siboga" Expedition. Stat. 204. S. E. of Celebes. 75—94 M.

Male colony.

Coenoecium consisting of a dense basal portion which forms a continuous encrustation

over the substratum, and of stiff, erect and slightly branched tubes, the foreign inclusions of which are more numerous than in the other species. Cavity of erect branches continuous, originating from the irregular cavity of the basal encrustation, into which the zooids can be retracted. Orifices widely infundibuliform, with a tendency to assume an alternate arrangement on two opposite sides of the branch, produced into a few moderately long peristomial filaments. Zooids dimorphic, consisting of neuters and males.

Neuter individuals with an elongated metasome, the stalk originating nearly from its aboral end; gonads absent, or represented by mere vestiges, or perhaps occasionally developed into functional testes. Tentaculiferous arms four pairs, apparently without end-bulbs and vesicles. All parts of the epidermis are densely pigmented.

Male individuals with conical body, which passes continuously into the stalk; alimentary canal vestigial; testes two, occupying most of the metasome and part of the stalk, and opening in the same position as the ovaries in the other species. Arms reduced to a single pair, without tentacles, their epidermis being crowded with large, highly refracting vesicles. Epidermis highly pigmented.

In both kinds of individuals the stalk is excessively long and slender, and apparently produces buds in great profusion.

IV. COENOECIUM.

It has been pointed out above that excellent specific characters are afforded by the coenoecium, which, however, has a well marked generic character. It is in all cases provided with a number of definite orifices, which in the species investigated, are usually bordered by one or more peristomial processes; and it is entirely composed of a series of superposed lamellae of more or less pronounced orange colour and of gelatinous consistency, as described by M'Intosh (**87**, p. 5) in the type-species. Many of the lamellae include various foreign bodies, such as Foraminifera, Sponge-spicules, particles of mud and so on, to an extent varying with the species. These lamellae closely resemble the rings which compose the tubes of *Rhabdopleura*. A careful examination of the free portions („peristomes") of the tubes in that genus (Pl. II, fig. 19) shews that the rings are not unbroken, but that each is interrupted by an oblique suture. The suture is easily seen when it is on that side of the ring which faces the observer (*a*), less easily when it is necessary to focus through the tube in order to see it (*b*), and may be difficult to distinguish when it lies on either edge of the tube (*c*). I believe, however, that the suture is a typical feature of the tube-ring; and that it indicates that the zooid, in constructing a new ring, begins at a definite point and works round the entire periphery of the tube until it returns to its starting point. It may be presumed that the part of the new ring first secreted has by this time somewhat hardened, so that the junction of the first- and last-formed part of the tube is indicated by the suture. This point escaped the notice of Sars (**72**, p. 3), who supposed the rings of the peristome to be uninterrupted, while he figures the sutures (Pl. I,

fig. 9) in the rings which constitute the creeping portion of the tubes. LANKESTER (**84**, p. 626) also emphasises this supposed difference between the peristomial rings and those of the attached parts of the tubes. The sutures of the peristomial rings are, however, clearly described and figured by SCHEPOTIEFF (**04**, p. 6, Pl. I, fig. 3).

There can be little doubt that the tube-rings of *Rhabdopleura* are successively constructed by the proboscis or buccal shield, as stated by LANKESTER (pp. 624, 626). It may fairly be assumed, with M'INTOSH (**87**, p. 6) that the coenoecium of *Cephalodiscus* is formed by the same organ, the greatly developed glandular epidermis of whose anterior side appears well fitted for this task.

C. levinseni. (Pl. II, figs. 11—13. Pl. IX, figs. 108—110).

The coenoecium of this species is characterised by the following features: — (I) by its definite law of growth; (II) by the existence of a distinct and separate tubular cavity for each of the zooids; and (III) by the prolongation of this tube into a well marked free portion or peristome, the orifice of which has a characteristic oblique form. These features are illustrated by Pl. I, fig. 10 and Pl. II, figs. 11—13.

Fig. 12 represents the details of the peristome *A* of Fig. 11. The tube has an accurately cylindrical cavity and is lined by a certain number of longitudinally disposed lamellae, which are not shewn in this figure, although some of them are represented in fig. 13. The wall of the tube is specially thickened on the side which passes into the projecting lip of the orifice. This thickened side forms a sort of mid-rib, which clearly serves as a supporting structure. The lamellae of which the peristome is composed closely resemble the tube-rings of *Rhabdopleura*, as is well seen when they are examined in optical section (*e. g.*, left hand side of fig. 13). The ring then appears evenly convex distally, and concave proximally where it overlaps the next lamella. In the greater part of the peristome, the lamellae are very oblique, sloping proximally from the abaxial side, or side of the mid-rib. In the more proximal part of the peristome, they are broad, indicating a rapid period of growth; while more distally they become more crowded and irregular (fig. 12). They probably never form complete rings, but the majority of those which are not merely concerned in the construction of the mid-rib form half rings, starting from the mid-rib, passing across the whole of one of the lateral surfaces of the tube, and ending in a point on the axial side. This structure is illustrated by the lamella *a* in fig. 12. The deposition of these lamellae may be alternate, so that if *a* forms part of what may be termed, for descriptive purposes, the "right" wall of the peristome, *b* will form part of the "left" wall, the two lamellae overlapping at the mid-rib. Distally this arrangement is by no means constant; but in the proximal region of rapid growth the lamellae may alternate quite regularly for a considerable distance. When the peristome is examined from the axial side, the interdigitating pointed ends of the half rings are often conspicuously seen.

A glance at fig. 12 will shew that the lamellae which constitute the mid-rib are far more numerous than those which form the rest of the tube; and it will further be seen that this disparity is due to the fact that many of the lamellae are concerned exclusively in building

up the mib-rib. These are especially numerous in the distal part of the peristome; and the constant elongation of the mid-rib produced in this way thus results in the acquirement of more and more obliquity in the disposition of the tube-lamellae as growth proceeds.

The structures which have so far been described may be distinguished as the "primary lamellae". *Cephalodiscus* differs from *Rhabdopleura* in laying down additional series of "secondary lamellae", both on the inside and on the outside of the primary lamellae. On the inner side, these have a longitudinal arrangement (fig. 13), and their formation can be accounted for by the supposition that the zooid lines its tube by additional lamellae secreted by its proboscis. The external secondary lamellae may appear as a series of longitudinal layers running down the outside of the peristome (figs. 12, 13), or as a series of layers bridging over the interval between two diverging peristomes. Fig. 13 shews two young peristomes, of which that on the left is viewed laterally, while that on the right is seen from the abaxial side. Examining the angle between the two peristomes, it will be noticed that growth took place for some distance without the formation of any bridging lamellae; and this arrangement can be made out in most cases. After a time, however, intermediate lamellae are deposited; and some of these appear to be derived from each of the two neighbouring peristomes. On the extreme left side of the figure, some of the external secondary lamellae are seen as prolongations of the primary lamellae; but many of them are certainly independent formations. It is probable that the extraordinary length of the neck-region of the zooid, and the great mobility of the proboscis, in this species, are correlated with the length of the peristomes, the animal having the power of stretching its proboscis a certain distance down the outer side of its tube, during the deposition of these external lamellae.

The laminated structure of the coenoecium is further illustrated by figs. 108—110 (Pl. IX), representing sections transverse to the principal axis of the entire colony. Fig. 109 shews parts of seven zooecia [1]), most of which are cut more or less transversely; although *c* and *e* are cut longitudinally, *c* through the wall of its peristome. In fig. 110, which shews the details of part of the same section, *b* points to one of the primary lamellae of the zooecium *e*; and it will be noticed that the primary lamellae are covered both internally and externally by secondary lamellae, some of the external ones being clearly contributed by the peristome *c*. The primary lamellae (*pr. l.*) of the zooecium *d* are also distinguishable. The zooecia *d* and *f* are separated from one another by a single series of primary lamellae (*pr. l'.*), indicating that the zooids do not each secrete a complete wall of their own, but economise material by making what use they can of the tubes of their neighbours in constructing their own zooecia.

Fig. 108 is a section of the basal region of another peristome, with an extensive development of both internal and external secondary lamellae. The two primary lamellae marked *pr. l.* are cut along nearly their whole length; and their sutural junction on the axial side is indicated in the lower part of the figure.

Foreign inclusions are not very numerous in the coenoecium of this species, but they are by no means absent, as is indicated by figs. 12, 13.

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1) I use the term "zooecium" without implying any homology with the structure known by the same name in Polyzoa. The term is etymologically applicable to *Cephalodiscus*, while its use in the Polyzoa may be defended merely on grounds of convenience.

The mode of growth of the coenoecium in *C. levinseni* is not at first sight apparent. The zooecia contain adult zooids, buds and developing embryos, any of which might conceivably play their part in the increase of the coenoecium or in the formation of new zooecia. I have no actual evidence that the embryos take any such part, but it is by no means impossible that they may add a few lining lamellae to the proximal end of the tube, where they mostly occur. The analogy of other fixed colonial animals suggests, however, that the embryos become free-swimming and thus have the function of originating new colonies. I cannot find any indication of bifurcation of the cavities of the coenoecium, or of the formation of diverticula which might give rise to new zooecia. The explanation which appears to me most likely is that the buds when liberated from the parent stalks make their way out of the orifices of the zooecia and crawl along the outer surface of the coenoecium until they find a suitable spot, where they settle down and commence to manufacture their own zooecia. The crawling movement would presumably be effected by means of the anterior surface of the proboscis, a mode of locomotion observed by Sars (**72**, pp. 9, 12) in the living *Rhabdopleura*. The proximal part of the entire coenoecium is considerably thicker than the distal part, and it consists of a larger number of zooecia. The increase in thickness can be accounted for by supposing that buds have commenced their tube-forming activity on some part of the external surface of the coenoecium. The supposition is also in accordance with the fact that the proximal parts of the zooecia are constituted partly by primary lamellae which are buried deeply within the coenoecium.

In one or two parts of the colony, forming either the tip of the main axis, or a lateral branch growing out from the axis, there are regions which are clearly young. This is indicated by the paler colour of the gelatinous substance, and by the thinness of the walls of the zooecia, which are here composed of primary lamellae only. The zooecia although less numerous than in the more proximal parts are already obeying the same law of growth. They contain young zooids (Pl. I, fig. 5), of the form described on p. 18, which are already engaged in budding, whilst their ovaries contain only immature eggs. In the more proximal parts of the colony, on the contrary, there is but little budding activity, while ripe eggs are produced by the ovaries, and most of the zooecia contain eggs and embryos. The bearing of these facts appears to me to be as follows. In the proximal part of the colony but few buds are produced, and accordingly the coenoecium increases in diameter comparatively little, the zooids expending most of their energies in the production of eggs, which develop into larvae destined to found new colonies. Nearer the growing tips there is a budding zone; the buds on escaping from the zooecia coming to rest near the bases of the existing peristomes, thus prolonging the coenoecium and increasing its diameter. If the outflow of buds is sufficiently great at any point remote from the apex of the coenoecium, a branch is formed. It must, however, be pointed out that I have searched in vain for positive evidence as to the initial stages in the growth of a new zooecium.

C. gracilis. (Pl. II, figs. 14—16. Pl. V, figs. 54, 55).

The slender coenoecium of this species, and its prostrate habit, are features which are in marked contrast with those of the robust and erect species which has just been considered.

The coenoecium consists of a delicate tube, bifurcating from time to time, and enclosing a cavity which is continuous throughout. The orifices, which appear to be confined to the ends of the branches [1]), are funnel-shaped openings, with irregular margins, and they are produced into a varying number of fine gelatinous "spines" or peristomial filaments. Similar filaments occur in the more proximal parts of the tube, where orifices appear to have been occluded by the deposition of gelatinous lamellae. Thus at *a* in fig. 15 three embryos are contained in a diverticulum of the main cavity which is completely closed distally, while the remains of filaments probably indicate that this was once one of the functional orifices of the coenoecium, when growth had not extended much beyond this point. Some parts of the tube are completely empty, while others contain numerous embryos, as well as zooids (adult and immature blastozooids), which are often so closely packed that it is difficult to trace the limits of the individuals. It is probable that the zooids, like those of *C. dodecalophus*, can wander at will through the cavity of the coenoecium. But the long, *Rhabdopleura*-like, stalk of this species probably enables the zooid to reach an orifice while the base of its stalk is still deep in the recesses of the coenoecium.

The foreign inclusions in the jelly are small and inconspicuous, but they include a considerable number of Diatoms and sponge-spicules. Many Diatoms are visible on the free surface of the coenoecium, and some of these are probably, from time to time, included in the jelly, in places where the deposition of fresh lamellae is taking place. It may be noted that the inclusions commonly rest immediately on an older lamella, and are covered by the next lamella.

The structure of the coenoecium resembles that found in *C. levinseni*, though its law of growth is much less definite than in that species. A consideration of fig. 16 will probably give a correct idea of its mode of growth. The figure shews two orifices (*a*, *b*) and three peristomial filaments (*c*, *d*, *e*). These filaments correspond with the "mid-ribs" of *C. levinseni*, but are much more developed than in that species. They project far beyond the orifices as cylindrical structures composed in the main of a series of overlapping conical primary lamellae, the shape of which is not complicated by taking part in the formation of a tubular zooecium. A few secondary lamellae, forming a transparent sheath to the process, occur in the more proximal part.

The tubular cavity of the coenoecium is being prolonged along these processes by the development of oblique primary lamellae (shewn in the lower part of fig. 16), similar to those of *C. levinseni* except in the fact that they take no share in the formation of the mid-rib, which precedes their formation. As the tube of the coenoecium becomes prolonged along the process, the mid-rib remains as a supporting rod passing along one wall of the tube. The lamellae composing this rod usually become darker in colour with advancing age; and as they have taken no part in the formation of the lateral walls of the coenoecium, the cylindrical supporting rod is sharply marked off from the rest of the coenoecium. . . . .

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1) Orifices are present in fig. 15 at the points marked by arrows. It is probable that others are really present as well; but all the more proximal ones appear to have been closed.

At *f*, in fig. 16, there is the edge of a lamella which is so prominent as to suggest that it was for a time the edge of an orifice (the lamellae between *f* and *b* have not been indicated in the figure). There can be no doubt that this was the case; and it will readily be seen that at this time the orifice was produced into the principal filamentous process *c*, which soon gave off the lateral branch *d*; while a third process *e* was formed at the opposite side of the orifice. With the increase in the length of the coenoecial tube the process *e* has been left unconnected with any orifice. The principal growth has taken place along *c*, which has doubtless increased meanwhile by the addition of new cones to its apex. The terminal orifice *a*, with its process *c*, now has a close resemblance to a peristome of *C. levinseni*. It consists almost entirely of primary lamellae, namely those of the mid-rib, and those of the rest of the tube. Secondary lamellae are at present but slightly developed.

Should further additions be made to the orifice *b* it is highly probable that they would take place along the process *d*, and a bifurcation of the coenoecium would thereby result. Fig. 15 shews that a considerable number of peristomial filaments may be developed in connexion with a single orifice.

Fig. 54 represents a longitudinal section through an orifice, with several peristomial filaments, of *C. gracilis*; while fig. 55 represents part of a transverse section through the coenoecium, more highly magnified. The figures both shew a considerable development of secondary lamellae on the inner side of the primary lamellae.

C. sibogae. (Pl. II, figs. 17, 18. Pl. IX, figs. 102, 103).

It must be remembered that the colony here described under this name contains male and neuter individuals, no females being present. It is thus necessary to consider the possibility that it may be the male form of *C. gracilis*.

The neuter zooids of *C. sibogae* are perfectly characteristic *Cephalodiscus* individuals except for the absence of functional reproductive organs. It can hardly be doubted that they take an important share in the secretion of the coenoecium, though I see no reason why the extraordinary male individuals should not contribute to its growth. But even taking account of this possibility, there seems no obvious reason why the characters of the coenoecium should differ to any great extent in the two sexes of the same species. The fact that there are definite differences in the coenoecia of the forms here described under the names of *C. gracilis* and *C. sibogae* is one of my principal reasons for regarding them as belonging to distinct species.

The coenoecium of *C. sibogae* consists of two very different parts: — (I) a denser portion which forms a continuous expansion over the rock on which it grows; (II) a series of upstanding tubes, fringed with numerous peristomial filaments, and arising from the basal encrustation (Pl. I, fig. 2).

The cavity of the coenoecium is continuous, that of the erect tubes passing into those of the basal encrustation. It is a remarkable feature of this colony that the zooids are nearly all retracted into the latter, so that the erect tubes are for the most part completely without zooids.

The stalks of the zooids of *C. sibogae* are excessively long and slender (as in *C. gracilis*). It seems to me by no means impossible that they may be sufficiently extensible to permit of the protrusion of the tentacles from the orifices while the bases of the stalks still remain in the basal encrustation. However this may be, it cannot be doubted that the densely massed zooids found in the basal part of this colony possessed during life the power of entering the erect tubes.

The tubes may be simple, bifurcated, or somewhat more branched. In one case which I have noticed, the tube trifurcated near its base, and two of these branches bifurcated a little later, making five branches in all. The branches have a certain straightness, which is in contrast with the sinuous and decumbent branches of *C. gracilis*, and is correlated with a firmer consistency of the jelly. Their colour is definitely orange (in spirit), those of *C. gracilis* having so little of the orange colour as to appear almost colourless. While the basal encrustation is for the most part free from foreign inclusions, all parts of the erect tubes take up an enormous number of particles of detritus or mud (which may possibly be faecal), as well as bodies such as the shells of Foraminifera and sponge-spicules.

The orifices are typically wide funnels which project from the walls of the tube, and have a tendency to assume an alternate arrangement. The peristomial filaments are stiffer and shorter than in *C. gracilis*. The lamellae which constitute the greater part of the tube are readily seen without staining. The upper half of Fig. 17 shews that they are convex distally and that they are of small size, a feature which may be regarded as correlated with the small size of the proboscis in this species. They are in fact not large enough to form even one half of the transverse circumference of the tube.

In *C. gracilis* (Fig. 16) on the contrary, the lamination is more difficult to make out without staining. The lamellae are not specially convex distally, and their arrangement recalls that found in *C. levinseni*, a tendency towards an oblique arrangement being noticeable, while the lamellae in many cases stretch across the whole of one of the lateral surfaces of the tube.

The mode of growth of the coenoecium of *C. sibogae* resembles that found in *C. gracilis*. The lower part of fig. 17 shews a funnel-shaped expansion, which was formerly the terminal orifice of the tube, its lower lip being still indicated by a prominent line *a*. This orifice was provided with the three peristomial processes *b*, *c*, and *d*, of which *d* lies in the wall which is furthest from the observer. With the prolongation of the wall of the tube by the deposition of fresh lamellae, the funnel-shaped orifice became narrowed, part of it remaining as an orifice *e*, in relation with the process *b*, the rest of it extending as a separate orifice along the process *d*. The process *c* thus became removed from any connexion with an orifice, and so ceased to grow. The process *d*, which in the lower part of the figure lies in the deeper wall of the tube, and in the upper part becomes nearly lateral, constitutes the principal skeleton of the tube, and is continued beyond its terminal orifice *i* as the process *n*. When the tube had reached a certain distance, a new peristomial process (*h*) was formed, which has become the support of the orifice *f*, most of which is concealed by the base of the process. The line *g* indicates the margin of the terminal orifice at a previous stage, although a considerable part of this funnel has now been closed by the onward growth of the tube, part of it persisting as the orifice *f*.

The end of the tube is a widely open funnel (*i*), of which *k* is the lower lip, and *l*, *m* and *n* are the peristomial filaments.

The filaments have a structure similar to that found in *C. gracilis*, consisting of a series of overlapping cones, with an occasional, very delicate, secondary lamella on their outer side. Some of the cones contain large numbers of minute granules, which are indicated in the upper part of the principal process *n*. Similar granules may occur in smaller numbers in the lateral lamellae.

It need hardly be pointed out that when the peristomial filaments become included in the wall of the tube, they retain the structure which they have at their first formation. The series of primary cones may thus be traced throughout the supporting sheletal bars which result from the modification of the peristomial filaments.

Secondary lamellae are not much developed in the erect tubes of *C. sibogae*, though a certain number occur on the outer side of the wall, and are probably in many cases responsible for taking up the foreign inclusions which form so conspicuous a feature of the species. The basal parts of the tubes may be lined by several layers of internal secondary lamellae.

The basal encrustation is a continuous film, with a smooth glistening surface, free from foreign inclusions. It moulds itself over all the irregularities of the stone on which the specimen is growing, and it is traversed by a continuous set of irregular cavities which contain the deeply pigmented zooids. The layer in actual contact with the stone is quite thin. A section of a part of the basal encrustation is shewn in fig. 102, and a part of the same figure, more highly magnified, to illustrate the details of the lamination, in fig. 103. The tube *a* is cut longitudinally, and shews on either side a well marked series of primary cones (*d*, *e*), of which the series *d* has given off a lateral branch, *f*, which has the same structure. In the interval between *f* and the upper part of *d* a few secondary lamellae can be recognized, while a certain number of similar lamellae line the cavities of the tubes. It should be noted, however, that some of the lamellae to the left of *d* are really primary lamellae cut tangentially.

It cannot be denied that the coenoecium of *C. sibogae* resembles that of *C. gracilis* in some respects; but the differences between the two specimens seem to be sufficient to indicate that they belong to distinct species, even making full allowance for the fact that they are of different sexes.

C. dodecalophus. (Pl. II, figs. 20, 21).

The general characters of the coenoecium are well illustrated by M'Intosh (**87**, text-fig. on p. 4, Pl. I, Pl. VII, fig. 1). Although offering an obvious generic similarity to that of *C. levinseni*, the coenoecium of *C. dodecalophus* differs from it in several noteworthy points. Instead of having a separate cavity for each zooid, it resembles that of *C. gracilis* and *C. sibogae* in containing an irregular, continuous, axial cavity, some parts of which may be empty, while others are crowded with zooids and eggs. The cavity communicates with the exterior by rounded orifices which are not borne by prominent peristomes (fig. 21). *C. dodecalophus* is characterised

by developing numerous bridges of jelly not only between adjacent branches, but between neighbouring elevations on the surface of a single branch. Although the orifices are sometimes mere holes in a flat surface (*b*), they are more often sunk in deep recesses (*c*) formed by the outgrowth or union of gelatinous lobes. The distinction between primary and secondary lamellae is at first sight not apparent, though a closer examination reveals traces of it. M'Intosh states (p. 5) that "all the spines are hollow", but in this there can be no doubt that he was mistaken. The spines in reality have a structure similar to that of *C. gracilis*, each of them being supported by an axis of denser jelly, which has a deeper orange colour than the more superficial parts. These axes, which appear to be hollow in certain modes of illumination, are shewn by their arrangement to be supporting ribs. One of them, broken at its tip, is seen at *a* in fig. 21. It forms a support for the film of jelly between itself and the main branch, and it is continuous at its base with the irregularly arranged development of the same stiffer jelly which occurs in the main branch. It is characteristic of these supporting pillars that they do not reach the end of the lobe or spine which they support. The axis usually extends through about two-thirds of the spine or lobe, and then ends abruptly in a sharply marked rounded termination. This is not indicated in fig. 21, in which, however, the spine *d* is supported by an axis which extends nearly to the tip of its shorter branch, while the longer, more delicate branch of the same spine contains no axial support.

An examination of one of the larger spines (fig. 20) of the colony shews that the axis consists internally of a series of overlapping cones, which correspond with the primary lamellae of *C. levinseni*, but are more pointed than in that species, The darker axis is, however, completed by a series of thin secondary lamellae; while the rest of the lobe is, for the most part, constituted by very numerous secondary lamellae whose paler colour distinguishes them sharply from the central axis. Those terminal parts of the lamellae or spines which are not supported by an axis are composed entirely of pale secondary lamellae.

Many of the long spines are closely related to an orifice. Thus the spines *d* and *e* of fig. 21 are peristomial filaments of the orifice which is seen to their left. As was the case in *C. gracilis*, many of the spines which do not at first sight appear to belong to an orifice may have been so related at an earlier period of growth, and may have lost that connexion by the subsequent deposit of secondary lamellae.

The process shewn in fig. 20 has given off a broad triangular lobe on its right side. The axis of this is constituted by characteristic conical primary lamellae, which, however, have not acquired the deeper colour seen in the larger axes.

The mode of growth of the coenoecium of *C. dodecalophus* is not quite apparent. There is no indication that the secreting part of the proboscis has the extraordinary mobility characteristic of *C. levinseni*. The stalk is moreover very thick and short, which would at first sight appear to forbid the assumption that the proboscis can be protruded far beyond the orifices of the coenoecium. It must, however, be remembered that the stalk of *C. dodecalophus* possesses a great development of longitudinal muscles, and that its epidermis and basement-membrane are usually very much wrinkled (Pl. XIII, fig. 169). This indicates contractility; and it may fairly be suggested that the stalk is capable of great elongation, so that it might

be possible for the zooid to keep the tip of its stalk, with its series of buds, in the shelter of the coenoecium, and to crawl on the anterior surface of its proboscis as far as is necessary to enable it to add gelatinous lamellae to the spines and other processes of the coenoecium.

A considerable number of Foraminifera and other foreign inclusions occur in various parts of the coenoecium of this species.

V. EXTERNAL CHARACTERS OF THE ZOOIDS.

Omitting for the present the males of *C. sibogae* which must be treated apart (see Sect. XV), all the species of the genus shew the typical *Cephalodiscus* character, differing from one another only in the relative size and in the shape of the several parts. The zooid consists of the three fundamental regions (I) the buccal shield, with part of its supporting neck, together homologous with the proboscis of Balanoglossus; (II) the collar, produced dorsally into 4—6 pairs of tentaculiferous arms, and ventrally into the lower lip or operculum; and (III) the metasome or body, continued into the stalk, which produces buds from its distal extremity.

MASTERMAN (**97**, 1, p. 290 f.) speaks of the three primary regions as "protomere", "mesomere" and "metamere", and of their cavities (**98**, 2, p. 516) as "protocoele", "mesocoeles" and "metacoeles" respectively. WILLEY (**99**, 2, p. 314) has pointed out that the use of the term "metamere" in this special sense is inadmissible, and replaces it by "opisthomere". I shall for the most part refer to the three regions as "proboscis", "collar" and "metasome" respectively, the last a term which is used by several authors in describing *Phoronis*.

C. dodecalophus (cf. Pl. IV, fig. 42). The general appearance of the zooid is well known from the admirable figure given by M'INTOSH (**87**, Pl. II). The proboscis forms an antero-posteriorly [1]) flattened disc, which in a front view usually overlaps the whole of the collar except the distal parts of the tentaculiferous arms or plumes, also concealing the mouth and the external apertures of the gill-slits and collar-canals. Its ventral half bears a conspicuous narrow band of reddish pigment, which forms a curved line, with dorsal concavity, extending transversely across the organ [2]). The body is ovoid and relatively short, the stalk originating from its antero-ventral surface, some way from its aboral end. The short and extremely muscular stalk is usually directed transversely to one side, or towards the mouth. Its epidermis is thrown into numerous, deep, transverse wrinkles, doubtless caused by the contraction of the muscles (see Pl. XIII, fig. 169). It seems obvious from this fact that the stalk of the "Challenger" specimens is in a highly contracted condition. It may reasonably be inferred that during life it is capable of a much greater amount of elongation, and it may be presumed that it then frequently places itself in a position parallel to the long axis of the body, with its distal end directed away from the mouth. This position is sometimes actually observed (M'INTOSH **87**, Pl. III, fig. 1); it is the position in which the other species are commonly found; and it

1) The sense in which I use terms descriptive of the surfaces and of the principal planes is indicated on p. 23.

2) This curved band of pigment has been erroneously represented as the mouth in a certain text-book.

is moreover the position in which stalk and body lie in immature buds. *C. dodecalophus* has six pairs of tentaculiferous arms, each of which ends in a swollen bulb containing remarkable refringent vesicles.

C. levinseni. (Pl. I, figs. 5, 6. Pl. III, figs. 23, 24).

In their old condition, the zooids of this species are characterised by having an extremely elongated, cylindrical form (Pl. I, fig. 6; Pl. II, fig. 11; Pl. IV, fig. 33), the apparent length, however, being commonly greater than the real length, in consequence of the fact that the somewhat coiled distal end of the stalk, sometimes bearing a bud, together with several large embryos, usually form a mass having the same diameter as the body, and so closely applied to its posterior end that the limit between this mass and the body is not at once made out. The elongated masses seen in the cavities of the coenoecium in fig. 11 thus consist, in most cases, of zooid + stalk + bud (if any) + embryos. The extreme elongation of the old zooids is, however, seen in the sagittal section shewn in fig. 33; from which it will be noticed that the arms pack themselves away, during retraction, so as to form a continuation of the cylindrical form of the rest of the zooid.

In old individuals the stalk is always directed away from the mouth, and is usually spirally coiled, the coiling being accompanied by some twisting round the longitudinal axis of the stalk, as is indicated by the direction of the muscle-fibres (fig. 6) In younger blastozooids (fig. 5), the proportions of the body tend to approach those of *C. dodecalophus*. Their stalk originates relatively much nearer the oral end of the body, so that the bend of the alimentary canal lies in a caecum of the body-wall which projects a considerable distance beyond the origin of the stalk. As moreover the stalk is commonly carried in such a way that it lies asymmetrically on one side of the body, pointing forwards, and with its distal end sometimes overlapped by the proboscis, these young individuals have a resemblance to the adult *C. dodecalophus* which is not shared by the adults of their own species.

Buds are not produced in great profusion, although it may be suspected that in a more actively growing colony, they would be more numerous. The old individuals, in which the production of eggs is energetically taking place, usually have no buds at all. The specimen, with young ovaries, shewn in fig. 6 has a single bud; and buds are certainly more numerous in the two or three regions where the coenoecium has an immature character, at or near the tips of its branches. These regions contain relatively young blastozooids, which have not yet acquired the elongated cylindrical form of the adults.

One of the most singular and characteristic features of *C. levinseni* is the form of its proboscis. This is not only relatively large, but it has an extraordinary amount of mobility, a peculiarity correlated with the unusually long neck, or proboscis-stalk, of this species. It commonly (during retraction) forms a sort of mantle, wrapping round a considerable part of the mass of arms and tentacles, as shewn in fig. 6. A glance at this figure will reveal the singular fact that as compared with other species, the pigment-line is upside down; and fig. 11 also shews various cases in which the position of the pigment-band is not what one would expect it to be.

Fig. 33, which is a sagittal section through the body and collar, shews no trace of the connexion of the two parts of the proboscis which are seen respectively anteriorly and posteriorly, with the rest of the animal.

These curious phenomena are due to the great length of the neck (figs. 23, 24, 139), which can be twisted into almost any position, either by being simply bent out of the median plane, or by being not only bent but also twisted round its own longitudinal axis. In buds and young blastozooids, and in some of the old zooids, the position of the proboscis is normal; that is to say, as in other species of *Cephalodiscus*. A case of this kind is represented in fig. 34. The neck here appears short and thick, though indications are not wanting, in the folding of the dorsal epidermis, that a considerable amount of contraction has taken place. It is not difficult to imagine that the basal, cylindrical portion of the proboscis in fig. 34 could, during life, be considerably elongated, and the discoidal portion rotated round an angle of 180° so as to bring the pigmented line to the dorsal side and the real dorsal portion of the disc to the ventral side. This is what has taken place in Pl. IX, fig. 101 and in Pl. XI, fig. 139. If the rotation be not so complete, — for instance, if it extend only to 90°, — the pigment-line assumes a more or less longitudinal position, as in several of the zooids seen in fig. 11. In the reconstructed individual shewn in figs. 23, 24 the elongated neck extends straight forwards, the discoidal portion looking in the same direction. This individual exhibits another phenomenon which is of common occurrence in this species, though something of the same kind may also take place in *C. dodecalophus*. By special contractions of the strong muscles which extend from the septum dividing the first from the second body-cavities, part of the glandular anterior epidermis of the proboscis may be deeply infolded. Sections of the proboscis of individuals in which this has taken place are sometimes difficult to interpret.

In the individual shewn in fig. 33 the neck is simply bent to one side, so as to have a direction at right angles to the median plane. The lateral portions of the mantle-like proboscis, with the ends of the pigment-band, have thus in this sagittal section a relation which they should normally have in a transverse section.

The arrangement of the body-cavity of the proboscis materially helps in the interpretation of sections of this species. Here, as in all other cases, the body-cavity extends to the extreme dorsal end of the organ (figs. 34, 42, etc.), where it is spacious; while it invariably disappears before the pigment-band is reached. The ventral lobe of the proboscis consists of a double layer of epidermis, the layer next the mouth being very thin, but the two layers are in close contact with one another without being separated by any part of the first body-cavity.

It should further be noted that the mobility of the neck in *C. levinseni* begins in front of the notochord and of the septum between the first and second body-cavities. Thus in the sagittal section, fig. 33, in which the anterior part of the neck is bent entirely out of the median plane, the symmetrical position of the central nervous system (*c. n. s.*), of the notochord (*nch.*) and of the pericardium (*per.*) has been in no way affected.

There are six pairs of arms in *C. levinseni*, as in *C. dodecalophus*; but I have not observed any indication of vesicle-bearing end-bulbs in the adults or at any stage in the growth of the buds.

C. gracilis. (Pl. I, figs. 4, 7. Pl. III, fig. 22).

This species differs from the two preceding in the *Rhabdopleura*-like slenderness of its stalk and in the profusion with which it produces buds (fig. 4). The stalk is, moreover, nearly always carried in what may be regarded as its primitive position, forming a continuation of the principal axis of the body.

Fig. 7 shews a side view of a zooid of this species, with rather unusually short stalk, and only a single bud. Fig. 4 represents a mass of buds and young blastozooids, of a kind commonly found in the cavity of the coenoecium of this species.

C. gracilis normally possesses five pairs of arms. End-bulbs, bearing refringent vesicles, are present in the first pair of arms at least, and sometimes in the second and third pairs, in the buds (figs. 30, 32). They may persist in the adult, but they appear to be sometimes absent.

C. sibogae. (Pl. I, fig. 3. Pl. VII, figs. 72—76).

My examination of this species has been interfered with by the failure of the spirit to penetrate satisfactorily into the deep lying cavities of the basal coenoecium containing the zooids. But in spite of this drawback, some of the main facts appear to be beyond dispute.

The colony is remarkable for an extraordinary dimorphism of the zooids. The coenoecium contains (I) neuter individuals, of the normal *Cephalodiscus* type, but usually without reproductive organs (which are, however, indicated in their young condition, while they are still immature buds); (II) male individuals, of an entirely peculiar character.

(I) Neuters.

These resemble the female individuals of *C. gracilis* in many respects, notably in the slenderness of the stalk. One of them is shewn in fig. 3, in which, however, only a portion of the excessively long stalk is present. They appear to differ from the zooids of *C. gracilis* in the following respects, in addition of course to the sexual difference:

(*a*) The proboscis is smaller, in *C. sibogae.*
(*b*) There are four pairs of arms, in which I have not observed vesicle-bearing end-bulbs.
(*c*) The greater part of the zooid is extremely dark in colour (almost black), in old individuals, owing to the presence of an unusually large quantity of pigment in the epidermis.
(*d*) The body is more elongated; and in old zooids may be extremely elongated.
(*e*) The stalk originates nearer the aboral end of the body. It is extremely long (many times the length of the body) and is indeed so long that I have not succeeded is disentangling the masses of stalks sufficiently well to trace the full length of an individual stalk.
(*f*) The operculum is larger, although this can only be seen satisfactorily in sections.

(II) Males.

I reserve a fuller account of these extraordinary individuals for a later part of this Report (Sect. XV). The full grown male (figs. 75, 76) possesses a typical proboscis, with the usual pigment-band. The collar is not produced into an operculum and bears only a single

pair of arms, which are without tentacles. In young males, the epidermis of the arms, except for a short region at the base, is entirely filled with refringent vesicles (Pl. IX, fig. 99), similar to those which occur in the terminal bulbs of the arms of *C. dodecalophus* and of the young *C. gracilis*. These vesicles appear to have been used up in some of the old males. The epidermis of the male, as in the case of the neuter, generally contains a great quantity of pigment. The body is large, and is almost entirely filled by a pair of enormous testes. The alimentary canal is vestigial.

VI. METHODS AND GENERAL ANATOMY.

In this Section I give a short description introductory to the Sections dealing with the special anatomy of the regions and organs.

My study of the structure of *Cephalodiscus* has been greatly facilitated by the use of solid reconstructions made from series of sections. The method which has been of most service is the one which was introduced by my friend Professor J. GRAHAM KERR (**01**, p. 5) and improved in some particulars by the late Mr. J. S. BUDGETT (**02**, p. 318). The principle of the method consists in drawing the sections on plates of finely ground glass, of uniform and suitable thickness, and immersing the superposed plates in a liquid having the refractive index of the glass. The liquid employed was a mixture of fennel-oil and cedar-wood-oil, as recommended by BUDGETT; and the proportions of the mixture which I have found it convenient to use are two parts of unthickened fennel-oil to one part of cedar-wood-oil. In this way a transparent reconstruction is obtained, in which different organs are brought out if they have previously been coloured with ordinary water-colour paints. Opaque colours, such as vermilion, can be used where it is desired to see only the outer form of an organ; and transparent colours in cases in which it is necessary to see internal details. Figs. 22—24 are in the main from reconstructions prepared in this way.

KERR's method can be most strongly recommended for many purposes; but finding that in some complicated cases, a more tangible amount of solidity was required in a reconstruction, I turned my attention to a form of modelling clay known as "plasticine". This clay has the advantage of not drying up, and of thus retaining its softness for any length of time. Thin plates of the plasticine can readily be prepared by pressing the substance on a smooth surface (such as a piece of paper), and removing the irregularities from the upper side of the plate by means of the back of a scalpel. The sections are drawn with a camera lucida on thin paper, and their outlines cut out with scissors. The paper pattern is pressed on the plasticine plate, which is then cut to the shape of the section with the point of a mounted needle.

The plates are superposed (removing the paper from the lower plate just before adding a new one), taking care to smooth off the edges and to fill up irregularities after the addition of each plate. The completed reconstruction, if carefully made, is a faithful reproduction of the original. The method does not differ in principle from the wax-plate method which has previously been used; but among its advantages are its great cheapness, and the ease with

which the plasticine plates can be prepared. A more striking advantage is that the flexibility of the material makes it posible to rearrange the position of the parts of the completed restoration. One of the great difficulties in dealing with *Cephalodiscus* is that such organs as the arms, the operculum, and the proboscis may overlap one another in such a way as to make it impossible to obtain a view suitable for drawing, or in which all the parts can be seen with the necessary clearness. A reconstruction prepared as above indicated overcomes many of these difficulties. The ventral lobe of the proboscis can be turned forwards so as to expose the operculum, the operculum can be turned down so as to shew the mouth, and the arms can be untwisted or straightened out: — and all this without putting any of these parts into a position which cannot be assumed during the life of the animal. Thus fig. 25 is a reconstruction made from the originals which are shewn in figs. 43—53, but it will be seen that the positions of the operculum and of the ventral lobe of the proboscis were modified after the completion of the model. The proboscis was also slightly rearranged in fig. 22, in order to shew the complete outline of the operculum.

A further advantage of the plasticine method is that a reconstruction made from oblique sections can be cut in a new plane, so as, for instance, to obtain a median sagittal section.

In studying the general anatomy of *Cephalodiscus*, one cannot but be struck with the constancy of the morphological type throughout the genus. The number of tentaculiferous arms indeed appears to depend on the species, but in other respects the organs already known to exist in *C. dodecalophus* are found, with practically no variation, in all the species — a fact which speaks for the high specialization of the genus. Differences in degree of development are, however, well marked; and indeed the species of *Cephalodiscus* have well defined characters of their own. But any one of the species would serve as well as any other to give a good idea of the essential generic characters.

The most fundamental fact in the structure of *Cephalodiscus* is the division of the body into the three regions, proboscis, collar and metasome; the proboscis containing an unpaired body-cavity, and each of the other two divisions containing its own paired body-cavities.

The disposition of the three regions is, however, by no means simple, since each of them is specially developed in relation with some plane or axis which does not correspond with the morphological principal axis of the animal. But an initial difficulty in describing the facts is that it is not agreed what is the correct orientation of the Pterobranchia as compared with the Enteropneusta. *Cephalodiscus* differs from Balanoglossus in the approximation of the anus to the mouth, and in the extension of the alimentary canal into a *U*-shaped loop. It can hardly be contested that the region characterised by the central nervous system and the apertures of the oviducts is dorsal; and it appears to be natural to regard the alimentary canal as extending into an enormous ventral extension of the body, as in *Phoronis*. If this be the correct orientation, the morphological posterior end of the animal is indicated approximately by the anus.

This is not the view which is adopted by Masterman (**98**, 2, p. 513), who considers that "the pedicle is morphologically the hind end of the body", and that the study of the buds favours this interpretation. It appears to me on the contrary that the disposition of the alimentary canal in immature buds indicates that the stalk is a ventral appendage.

The text-figure 1 is based on the sagittal section of an advanced bud of *C. dodecalophus* shewn in Pl. XIII, fig. 181. The proboscis, the collar and at least half the alimentary canal in this specimen have a position which closely corresponds with the relations of these parts in Balanoglossus. The principal morphological axis may be regarded as the line of intersection of what is marked as the "frontal" plane with the sagittal plane of the figure itself. It will then be seen that in this figure the pharynx (*ph.*) passes in an antero-posterior direction, giving off the notochord (*nch.*) forwards from its dorsal side, and passing posteriorly into the oesophagus (*oes.*) and stomach (*stom.*). This organ has a conspicuous dorsal caecum (*stom. d. c.*), while a smaller lobe extends a short distance forwards on the ventral side of the oesophagus. The dorsal line of the metasome is shortened, so that the intestine (*int.*), which opens from the second stomach (*stom.*^{2}), passes dorsally and a trifle forwards, to open at the anus (*an.*) which has been shifted into a somewhat dorsal position.

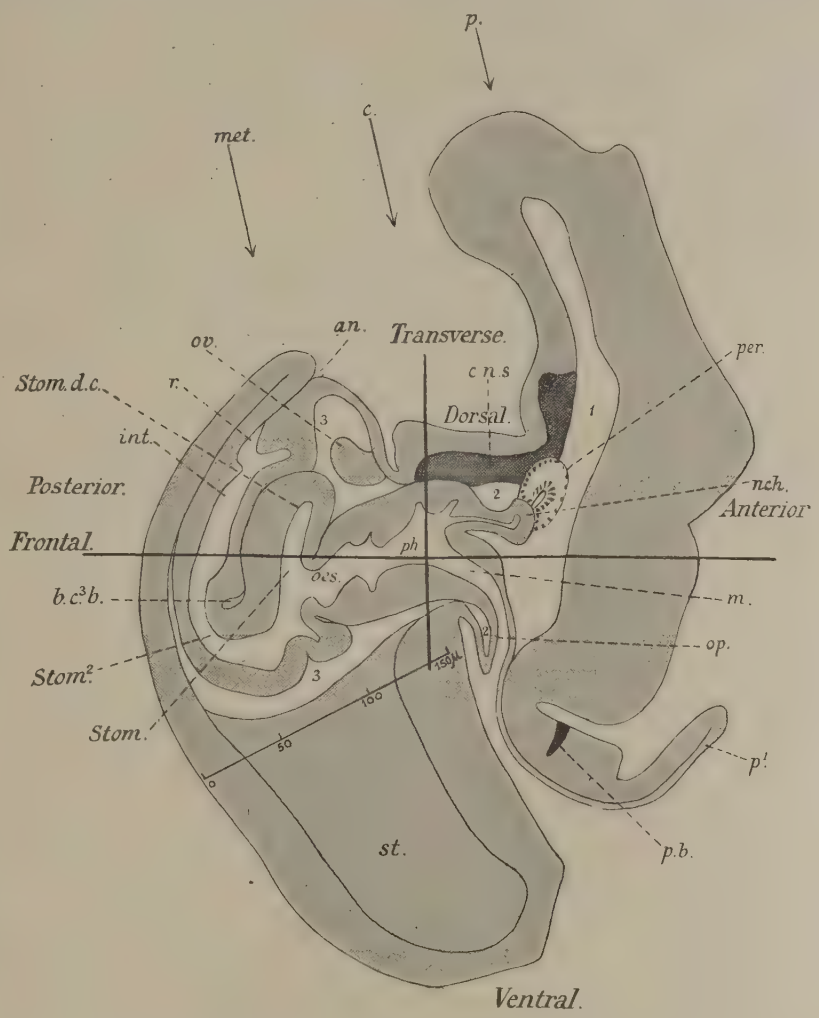

Fig. 1. — *C. dodecalophus.* Median sagittal section of an advanced bud (after Pl. XIII, fig. 181), to illustrate the terminology used in this Report. The anterior, posterior, dorsal and ventral surfaces and the transverse and frontal planes are indicated: — *p.*, proboscis; *c.*, collar; *met.*, metasome; 1, 2 and 3, their respective body-cavities; *b.c.*^{3}*b.*, the part of the metasomatic cavity included in the loop of the alimentary canal; *p'.*, ventral lobe of proboscis; *p.b.*, its pigment-band; *per.*, pericardium; *m.*, mouth; *nch.*, notochord; *ph.*, pharynx; *oes.*, oesophagus; *stom.*, stomach; *stom. d. c.*, dorsal caecum of stomach; *stom.*^{2}, second stomach; *int.*, intestine; *r.*, rectum; *an.*, anus; *c.n.s.*, central nervous system; *op.*, operculum or lower lip; *ov.*, ovary; *st.*, stalk.

Comparing the text-figure with the sagittal section of the adult (Pl. IV, fig. 42), in the same species, it will be seen that the alimentary canal in its definitive arrangement has its ventral flexure more strongly marked than in the bud. The morphologically dorsal surface of the pharynx now faces, for the most part, posteriorly, and its ventral surface anteriorly, although the part which immediately succeeds the mouth has its dorsal wall in its original morphological position. The pharynx is in fact ⌐-shaped, a right-angled bend having been developed owing to the ventral flexure of the alimentary canal.

The differences between what I regard as the more primitive condition shewn by the bud and the adult arrangement are in reality very slight, and can easily be accounted for by differential growth. The outlines of the text-figure are taken from a camera lucida drawing, the scale of which is indicated. Comparing this with fig. 42 it will be seen that while the diameter of the stalk of the bud, at its base, slightly exceeds 150 μ., that of the adult stalk, in the same relative position, is less than 200 μ., in spite of the thickening which it has no doubt experienced as the result of the contraction of its longitudinal muscles. There is thus but little increase in the thickness of the stalk of the adult, as compared with that of the bud, the principal increase in size of which has been due to an elongation of the metasome along an axis which is indicated in the bud by a line passing through the middle of the pharynx, oesophagus and part of the second stomach. This has resulted in the separation of the base of the stalk from the mouth, and in the outgrowth of the caecum of the metasomatic wall containing the bend of the alimentary canal. With this growth has been associated a ventral flexure of the pharynx just behind the mouth; a strongly developed dorsal groove which is present in this region remaining to mark the point at which flexure took place as the dorsal diverticulum (fig. 42, *div.*) of the pharynx. It thus follows that while there is hardly any distortion of the primitive symmetry in front of the line indicating the transverse plane in the text-figure, and comparatively little on the dorsal side of the horizontal line indicating the frontal plane, the principal modification of the axes of the adult body is due to alterations in the lower left quadrant of the text-figure. The pharyngeal limb of the alimentary canal has to a large extent lost its antero-posterior direction, and has assumed a position nearly parallel to that of the intestinal limb.

The correctness of this orientation is confirmed by the consideration of the mesenteries of the metasome. The dorsal mesentery is confined to the region between the two limbs of the alimentary canal, while the ventral mesentery extends into the stalk, carrying with it what may for the present be termed a loop of the ventral vessel. Indications of the anterior (*a. v.*) and posterior (*p. v.*) limbs of this vascular loop are seen in fig. 42.

A further confirmation of the orientation here adopted is afforded by a consideration of horizontal sections on the dorsal side of the line indicating the frontal plane in the text-figure. A section in this plane of a young bud was figured by me (**87**, p. 39) some years ago, and demonstrates the Balanoglossus-like structure of the animal. But even in the adult zooid, horizontal sections in the same region still shew the coelomic cavities in a Balanoglossus-like arrangement, as is evident from figs. 154, 155 (Pl. XII), which though not actually fully grown, do not differ from the adult condition in this respect. A transverse section of a young *Cephalodiscus* is thus one which passes along the line so marked in the text-figure. It is convenient to describe a corresponding section which passes through the long axis of the adult as "transverse", although it is obvious from what has been said that it will not cut all the organs of the metasome in a strictly transverse plane.

Adopting this view, it may be said that the proboscis is flattened in an antero-posterior direction to form the great buccal disc. The collar forms a ring which would be transverse were it not for the fact that its dorsal region is much more developed than its ventral region.

The apparent obliquity of the body-cavities in young buds (Pl. XIII, fig. 174) becomes intelligible if it is assumed that the antero-posterior axis cuts the first and second body-cavities at right angles.

The dorsal region of the collar is distinguished by the development of the central nervous system (fig. 42, *c. n. s.*) which also extends on to the adjacent parts of the proboscis; and of the paired tentaculiferous arms on either side of the middle line. Ventrally the collar gives rise to the enormous lower lip or operculum (Pl. III, fig. 25, *op.*), a structure which must be of great importance in feeding, and in regulating the action of the gill-slits and collar-canals. The collar-cavities, as seen in a nearly sagittal section (fig. 42) are much larger dorsally than ventrally, since they have to give origin to the cavities of the arms. A section which cuts the whole of the main part of one of the collar-cavities thus has the form seen in Pl. IV, fig. 36 or Pl. XII, fig. 151.

The long axis of the metasome is at right angles to the antero-posterior axis. In describing the parts of the metasome and stalk I shall consider the stalk as lying in the position in which it occurs in buds and in the adults of most of the species; that is, in the position shewn in Pl. I, figs. 4, 6, 7. The pharyngeal side of the metasome, or that from which the stalk originates, is the "anterior" side; while the rectal side is the "posterior" side. The most "ventral" part of the body is, for descriptive purposes, the end of the hernia-like projection containing the bend of the alimentary canal, although morphologically it more nearly corresponds with the base of the stalk.

The mouth (fig. 25, *m.*) is an orifice to which the food is conducted through a passage formed, on each side of the proboscis-stalk, by the posterior wall of the ventral half of the proboscis and the anterior wall of the collar, constituted by the arm-base (*a. b.*) and the operculum or lower lip (*op.*). It leads into a pharynx (fig. 42, *ph.*) from which a single pair of gill-slits open to the exterior, laterally, but somewhat on the anterior surface of the body. The external orifice of the gill-slit (fig. 25, *g. s. r.*) is immediately ventral, or morphologically posterior, to that of the collar-canal (*c. c. e.*) of the same side of the body; and both orifices lie so close to the base of the operculum that it is only in favourable specimens that they can be seen from the outside without being viewed through the ventral lobe of the proboscis, or through the operculum, or through both these structures.

The pharynx passes into the oesophagus (fig. 42, *oes.*) and these two parts together form the commencement of the anterior limb of the *U*-shaped canal. The opening of the oesophagus into the stomach (*stom.*) is usually borne on a large papilla which projects into the lumen of the stomach between the dorsal and ventral caeca of the stomach seen in the figure on p. 23. The second stomach (fig. 42, *stom.*^{2}) opens from the anterior side of the stomach, in the immediate neighbourhood of the base of the stalk (*st.*). It passes round the ventral border of the stomach, where it becomes continuous with the intestine (*int.*); this passes, in close contact with the posterior wall of the stomach, into the rectum (*r.*) the anterior wall of which is exposed to the body-cavity. The anus (fig. 22, *an.*) is a transverse slit on the dorsal and posterior side of the metasome.

A great part of the interval between the pharynx and the rectum is occupied (in female

specimens) by a pair of large ovaries (fig. 22, *ov. r.*, *ov. l.*), each of which leads by a pigmented oviduct (*ovd.*) to its external orifice, situated on the dorsal surface of the metasome, not far behind the end of the central nervous system. Between the pharynx and the rectum, in the middle line of the body, and consequently between the two ovaries lies the dorsal vessel (*d. v.*), which is the largest blood-space of the animal.

The above are the more conspicuous anatomical features of the zooid, and further details may be left for the Sections dealing with the several organs.

VII. PROBOSCIS.

The general characters of the proboscis or protomere, in the several species, have already been described (p. 17); and in particular attention has been called to the extraordinary proboscis of *C. levinseni*. The proboscis of that species is of remarkable mobility, owing to the presence of an unusually long neck or proboscis-stalk. The neck may be stretched out in the direction of the principal axis of the body (figs. 23, 24), carrying the discoidal part of the proboscis or "buccal disc" into an endless variety of positions. In fig. 24, the disc has the form of a somewhat complicated umbrella; but it may assume almost any position, and is very commonly turned upside down, so that its dorsal edge looks ventrally, and its ventral edge dorsally (figs. 101, 139), by the rotation of the neck round its longitudinal axis. These remarkable attitudes of the proboscis may make it a matter of some difficulty to interpret the sections of the anterior end of the animal; and the complication is often further increased by the retraction of the thick anterior wall of the disc into a strong fold (figs. 23, 24, 139), a habit which may also be noticed in some specimens of *C. dodecalophus*. The sagittal section, fig. 34, is one of the cases in which the proboscis has its normal position; but the extensible character of the neck is even here indicated by its thickness and by the folds in its walls.

In spite of these peculiarities of *C. levinseni* the proboscis has the same essential characters in all the species, not excepting the male individuals of *C. sibogae*. It may be remarked that the term "buccal disc", which has usually been employed in describing this part of the animal, is not exactly synonymous with "proboscis". The latter is a morphological term, indicating its relation to the similar organ in Balanoglossus. The "buccal disc", however, may include dorsally a part of the collar (fig. 42) although in *C. levinseni* it consists of the anterior end of the proboscis, the posterior end of which, with part of the collar, constitutes the neck or proboscis-stalk.

The relations of the collar to the proboscis will be described below, in the Section dealing with the collar. The proboscis itself invariably terminates in front in the enormous buccal disc, which is flattened in an antero-posterior direction. The anterior wall of the disc is composed principally of much elongated gland-cells, which give this wall of the proboscis a great thickness. As has been pointed out above (p. 9) there can be little doubt that the gland-cells have the function of secreting the gelatinous coenoecium. At the base of the gland-cells may be seen, in

the thickest part of the proboscis, a transparent layer (fig. 42) which I regard, with MASTERMAN (**87**, 2, pp. 342, 343), as nervous.

The unpaired proboscis-cavity (fig. 42, *b. c.'*) extends to the dorsal end of the buccal disc, the epidermis passing round this edge as a fairly thick layer. A similar arrangement is seen in the lateral edges of the dorsal half of the proboscis (figs. 111, 152). But ventrally to the insertion of the proboscis-stalk, the anterior and posterior walls of the proboscis rapidly come into contact, by the disappearance of the body-cavity in this region. The greater part of the ventral lobe of the proboscis is accordingly formed of two layers of epidermis in close apposition (fig. 42), the anterior wall consisting of a thicker epithelium, and the posterior wall of a very thin layer which passes into the ventral epithelium of the proboscis-stalk, and so to the upper lip.

In the region where the two epithelia of the proboscis are apposed, is invariably found a characteristic line of pigment (figs. 3—7, *p. b.*), which has a brilliant red colour in the spirit-specimens. This line forms a crescent, extending transversely across the ventral lobe, from edge to edge, and with its concavity directed dorsally. The pigment can readily be seen in sections (fig. 42), and it is clearly very resistent to the action of reagents. The pigment-line occurs very early in the young buds, in which the enormous development of the buccal disc is one of the most characteristic features (figs. 4, 9), and it is found in the males of C. *sibogae* (Pl. VII, figs. 72, 75, 76).

In a well preserved specimen of *C. dodecalophus* (Pl. XII, fig. 151), the pigment-line is related to a special modification of the epidermis on its dorsal side. The cells immediately adjoining the pigment are large protoplasmic cells. which have stained (with haematoxylin) less intensely than other parts of the proboscis. These are followed by a group of numerous minute nuclei in an area which is practically unstained. The deeply staining gland-cells of the anterior epidermis then follow, at first sparingly and, near the bend of the ventral lobe, associated with a considerable number of the minute nuclei already noticed. These become fewer in passing dorsally, and the part of the anterior epidermis which is uniformly tinted in the figure is constituted, up to about the reference-line *b. c'.*, almost entirely by the greatly elongated, densely staining gland-cells which extend from the nervous layer to the free surface of the epidermis. There are no gland-cells on the ventral side of the pigment-band.

It is difficult to decide what may be the physiological significence of the pigment-band and of its related cells. M'INTOSH (**87**, pp. 27, 34) suggests that the pigmented oviducts may be phosphorescent organs. No difference in colour can be noticed between the pigment in the pigment-band of the proboscis and that of the oviducts, in the sections shewn in figs. 149—151, and it is possible that there may be some relation between the functions of the two parts. So far as the proboscis is concerned, it is conceivable that the function might be that of vision, although the nerve-supply seems inadequate on that hypothesis, and it must further be remembered that *C. dodecalophus* is an abyssal form. But it seems very improbable that the oviducts, which have no distinct nerve-layer, can be used as visual organs. In the case of the proboscis, the function of the pigment, whatever it may be, is probably associated with a sensory function of some kind, as appears to be indicated by the presence of the numerous cells with small nuclei which occur in the region of the bend of the proboscis in fig. 151. The

sensory function claimed for the anterior epidermis of the ventral lobe may be connected with the deposition of the gelatinous layers which constitute the coenoecium. The lobe is obviously very mobile, as is indicated by the varying positions which it occupies in the preserved zooids. Since, however, neither the musculature of the proboscis nor the anterior body-cavity extends into it, its movements would seem to depend on protoplasmic contractions of the epidermis.

It is not improbable that the nerve-layer shewn at the base of the thicker parts of the anterior epidermis may extend as a thinner stratum into the ventral lobe, though I have not definitely proved that this is the case.

The ventral extremity of the anterior body-cavity extends, below the base of the notochord, as far as the upper lip (figs. 37, 42, 183; *u. l.*), which occurs immediately in front of the pharyngeal diverticulum (*div.*), from which the notochord originates (fig. 181). The relations of this ventral part of the proboscis-cavity to the upper lip and to the notochord suggest those of Balanoglossus, in which the corresponding part of the coelom gives rise to the median part of the "nuchal skeleton" or "proboscis-skeleton", and in certain species to the structure described by SPENGEL (**93**, p. 175; **03**, p. 280) as the "blumenkohlähnliches Organ", a structure to which WILLEY has given the name of "racemose organ" (**99**, 2, pp. 229, 260).

In certain positions of the proboscis (figs. 43—46) the ventral epidermis of that organ, in front of the mouth, forms the roof of the passage which encircles the proboscis-stalk, and conveys the food from the arms to the mouth. In passing from the mouth outwards this food-channel gradually ascends the proboscis-stalk, and becomes the deep groove (figs. 151—147, *f. c. r.*; fig. 155, *f. c. r.*, *f. c. l.*) which is bounded in front by the posterior epidermis of the proboscis, and behind by the thicker epidermis of the anterior side of the arm-base. The thin posterior and ventral epidermis of the proboscis thus has an important part to play in helping to define the cavity in which the food must pass from the arms to the mouth. The dorsal epidermis of the proboscis immediately in front of the end of the collar contains a strong nerve-layer (figs. 35, 37, 42) which is a direct continuation of the central nervous system.

The more important structures directly connected with the proboscis-cavity, or contained in it, are the notochord, the pericardium, the proboscis-pores, the glomerulus, and the muscles. Of these the notochord may conveniently be treated in Section XI dealing with the alimentary canal, while the muscles are described in Section XII.

Pericardium and proboscis-pores.

The pericardium was first figured by MASTERMAN (**97**, 2, figs. 2, 3, 14, etc.) who described it, however, as a blood-cavity. This account was criticized by me in a note (**97**) in which I contended that the pericardium (= "heart-vesicle") has the same relations as in Balanoglossus; and MASTERMAN has more recently (**99**, 2; **03**, p. 719) accepted this view.

The pericardium of *Cephalodiscus* closely resembles that of Balanoglossus. It may readily be found, in all the species, in contact with the dorsal wall of the proboscis, immediately in front of the tip of the notochord, and between the ends of the anterior dorsal horns of the collar-cavity. It appears to form a completely closed vesicle (Pl. XI, fig. 138; Pl. XIII, fig. 181) the posterior wall of which is invaginated into the lumen of the organ to form a space which,

on the analogy of Balanoglossus, must be regarded as a blood-space (fig. 181, *per. s.*) It will be seen from longitudinal sections (Pl. IV, fig. 33) that the pericardium more or less overlaps the tip of the notochord, which, in sections in other planes, may accordingly he completely encircled by the pericardium (Pl. XII, fig. 160).

The proboscis-pores, which are invariably two in number, have a constant relation to the pericardium (Pl. X, fig. 112; Pl. XI, figs. 137, 138; *p. p.*). The pore is in reality a tube of appreciable length; and in consequence of this fact SPENGEL (**93**, p. 470) prefers to term it the "Eichelpforte" (in Balanoglossus). In *Cephalodiscus* (figs. 112, 138) the epithelium of the tube which is situated nearer the middle line closely invests the wall of the pericardium. The outer part of the epithelium is intimately related to the anterior dorsal horn of the collar-cavity (*b. c.*^{2} *a.*).

In sagittal sections (Pl. XII, figs. 147, 148, *p. p. r.*; fig. 150, *p. p. l.*) it is seen that the direction of the tube is not vertical to the surface, but that it has an oblique course, the internal opening being dorsal to the external opening. The latter is situated close to the base of the first arm (Pl. XII, fig. 158), and slightly on its median side. The proboscis-pores traverse a part of the central nervous system, which is thus divided into an anterior and a posterior portion in any sagittal section passing through a proboscis-pore (figs. 42, 151).

MASTERMAN (**03**, p. 717) has described the proboscis-pores as opening into the outer ends of a transverse, crescentic furrow of the epidermis which he terms the "ectodermal pit". It is easy to find specimens of *Cephalodiscus* shewing appearances which resemble MASTERMAN's figures. Thus an "ectodermal pit" is obvious in Pl. XII, fig. 149; but I find that in this particular case, the proboscis-pore does not open into the continuation of the pit or furrow, but distinctly in front of it. In other cases (Pl. V, fig. 45), the relations are reversed, and a similar furrow is seen in front of the region where the proboscis-pore opens to the exterior. Remembering the extremely muscular character of the proboscis and collar I am inclined to think that these furrows are not constant structures, but are merely the result of crumpling of the skin caused by contraction.

Glomerulus.

I have previously stated (**97**, p. 345) that there appears to be some indication of a structure corresponding with the proboscis-gland or glomerulus of Balanoglossus; and MASTERMAN has recently (**03**, p. 720) described the organ in detail. I have nothing to add to MASTERMAN's account, and I have indeed not obtained any preparations which shew its relations so clearly as are indicated in his figures. Although I think it is probable, as MASTERMAN states, that it contains blood-spaces by means of which the pericardial sinus (Pl. XI, fig. 138, *per. s.*) communicates with other parts of the vascular system, I cannot obtain any certain evidence on this point.

The glomerulus (*gl.*) is shewn in Pl. IV, fig. 42 *(C. dodecalophus)*, Pl. VIII, fig. 93 (*C. sibogae*, neuter) and Pl. X, figs. 113, 114 *(C. levinseni)*; and its wall is doubtless to be regarded as a derivative of the epithelium of the anterior body-cavity.

VIII. COLLAR (including the arms and the operculum).

This division of the animal is not only one of the most characteristic and important parts of *Cephalodiscus*, but it is also the most difficult to understand thoroughly. The relations of its several parts, and particularly of the arms to the operculum, have not previously been adequately described.

It will be remembered that in Balanoglossus the anterior margin of the collar forms a projecting fold encircling the base of the proboscis-stalk. The ventral half of this fold may be regarded as constituting a lower lip, while the dorsal part is connected, in the middle line, with the anterior neuropore. In *Cephalodiscus* the neuropore is not represented, and the collar forms no projection in the median dorsal line above the base of the proboscis. Except for this interval, the whole of the anterior margin of the collar forms a strongly-developed fold, split up dorsally to form the arms, and ventrally constituting the operculum. It is necessary to insist on this last point because the base of the operculum is so narrow, and the flap itself is so commonly directed away from the proboscis, that the operculum might be taken to be a derivative of the posterior edge of the collar, as indeed I at one time (**87**, p. 43) supposed it to be. Its real relations can be most easily seen in *C. levinseni* (Pl. IV, figs. 34—36), in which the median ventral part of the collar-cavity is so long that it is at once apparent that the operculum is developed from its anterior margin. Unless this be recognized, it is impossible to form a clear conception of the relations of the arms to the operculum.

Fig. 25 (Pl. III) represents part of a plasticine reconstruction of *C. gracilis*, made from the series of obliquely sagittal sections some of which are shewn in Pl. V, figs. 43—53.

The ventral lobe of the proboscis of the reconstruction has, however, been turned dorsally, and the operculum itself has been folded in the opposite direction, in order to expose the mouth (*m.*). The bases of the five arms characteristic of this species are shewn, the first and second arms (*R.* 1, *R.* 2) having become free from the anterior collar-fold, while the third, fourth and fifth arms (*R.* 3—5) are not yet free, but are indicated by their food-grooves turned towards the mouth, and by their angular dorsal or external surfaces. The right lateral lobe of the operculum (*op.*) is here shewn in section, exposing the corresponding part of the collar-cavity.

The arm-bases form a gentle curve which is convex towards the mouth. The effect of this arrangement is that while the food-groove of the first arm faces almost dorsally, those of the second, third and fourth arms face anteriorly, and that of the fifth arm nearly ventrally. In passing away from the middle line, the fifth arm (in this specimen) rapidly becomes twisted round its own longitudinal axis, so that in the reconstruction fig. 22 (taken from the same specimen, but shewing more external portions of the arms and the whole of the right side of the operculum) its food-groove faces directly backwards, or towards the anus. The whole arrangement of the parts round the mouth shews that the proboscis and the anterior fold of the collar together form a highly efficient apparatus for conducting food to the mouth. The Diatoms and other minute structures which are actually found in the alimentary canal are

doubtless collected by ciliary currents induced in the first instance by the tentacles. It may fairly be assumed that the food passes along the grooves situated on the morphologically ventral or internal sides of the arms down to the arm-bases, where they enter a passage limited in front by the posterior wall of the proboscis and behind by the anterior collar-edge, which consists more dorsally of the common base of the arms, and more ventrally of the opercular flap. The operculum passes dorsally into the base of the last of the series of arms, to which it is related in such a way that the food-groove of that arm becomes continuous with the internal layer of epidermis of the collar-edge.

It will be noticed that in the reconstruction the food-grooves are represented as dying away before they actually reach the mouth. MASTERMAN (**98**, 2, p. 507) has given an elaborate account of the passage of these grooves, through the mouth, into the pharyngeal part of the alimentary canal; and his results are discussed below, in dealing with the mouth. Although the inner epidermis of the collar-fold is often a good deal wrinkled, I cannot agree with MASTERMAN that the food-grooves of the arms are continued as such into the mouth. Such sections as those represented in Pl. V, figs. 43, 45; Pl. VI, figs. 65, 66 and Pl. XII, figs. 145—147 shew that the arm-base has a perfectly smooth surface in regions where, according to MASTERMAN, grooves should be present. The food-channel limited by the proboscis and operculum is an arrangement so effective that it is hardly necessary to suppose that each food-groove must be continued independently to the mouth.

The lateral part of the operculum projects a considerable distance beyond the point where the fifth arm joins it. This is indicated, not quite successfully, in fig. 22, and is also apparent in fig. 25, in which the edge of the collar-fold is quite complete just ventrally to the base of the fifth arm, while the lateral part of the operculum is cut by the (sagittal) section in such a way as to expose its cavity. The same facts will be obvious from an inspection of the sections, Pl. V, figs. 50—53.

This lateral projection of the operculum is so situated as to overhang the external openings of the collar-canal (Fig. 25, *c. c. e.*) and gill-slit (*g. s. r.*). I think it cannot be doubted that the opercular lobe in question is functionally correlated with those apertures, and that it serves to separate the food-current passing to the mouth from the presumably exhalant current passing out of the gill-slit at least. The current through the collar-pore is probably sometimes inwardly and sometimes outwardly directed. The proper play of the tentacles and arms, and of the operculum itself, must depend on their being kept in a proper condition of turgidity. In the Enteropneusta there is actual evidence (SPENGEL, **93**, p. 475; cf. also RITTER, **02**) of the importance of a turgid condition of the collar-cavity. Now the collar-canal itself appears to have no sphincter muscles, and it seems to me probable that the lateral lobe of the operculum is important as one of the means of closing the external orifice of the collar-canal during certain conditions of the activity of that organ. Any excess of water which enters the pharynx is probably evacuated by the gill-slits; and as I suggested on a former occasion (**87**, p. 44) it is not impossible that this might have been the primitive function of the gill-slits of Chordata.

The structure of the collar may be further elucidated by a consideration of the actual sections on which the reconstructions, figs. 22, 25 (Pl. III), are based. The obliquely sagittal

sections drawn (Pl. V, figs. 43—53) begin with one which passes nearly medianly through the pharynx (fig. 43) and end with a section (fig. 53) through a plane in which all the five arms have separated from the arm-base. Two points must be noticed in interpreting these sections: — (I) the intestine appears to open into the middle of the posterior side of the stomach (figs. 43, 44). I find no trace of this arrangement (which has not been shewn in fig. 22) in other specimens of *C. gracilis*, and I have no doubt that it is due to an artificial rupture or to an abnormality: — (II) Owing to a strong lateral curvature of the body (which has not been brought out in fig. 22), the end of the metasome connected with the stalk becomes separated, in the sections, from the anterior end.

Fig. 43 represents a section, which passes somewhat to the left of the proboscis-stalk. The proboscis (*p.*) is thus completely separated from the collar. The operculum (*op.*) in this individual is directed forwards, and has the appearance of a lower lip. The dorsal part of the collar is produced in front into the left arm-base, with which the third (*L.* 3) and fourth (*L.* 4) arms are connected [1]). The collar-cavity (*b. c.*[2]) extends as a wide space into the arm-base, and is separated by an oblique septum from the third body-cavity (*b. c.*[3]). On the front side of the collar-cavity is the oral muscle (*or. m.*), a strong band of longitudinal muscle-fibres on the inner side of the anterior body-wall. The collar-cavity is interrupted by the mouth (*m.*), on the ventral side of which is the part of the cavity which extends into the operculum.

Fig. 44 represents a section which passes nearly through the middle of the proboscis-stalk. The first and second left arms are now continuous with the arm-base. The septum between the first and second body-cavities [2]) contains the notochord (*nch.*), starting from the anterior side of the median dorsal diverticulum (*div.*) of the pharynx, which extends completely up to the dorsal body-wall. The posterior wall of the dorsal part of the cavity contains part of the central nervous system (*c. n. s.*). In other respects the collar in this section resembles what was described in the previous section, except that it is now continuous with the proboscis.

In fig. 45, the middle line has been passed, so the collar-cavity is that of the right side. The right edge of the mouth has just been passed, and a strong oral muscle (*or. m.*), corresponding with the similar left muscle shewn in fig. 43, is seen to extend from the septum $^2/_3$ round the edge of the mouth to the anterior wall of the arm-base. The septum $^1/_2$ has a crenulated appearance, and from it radiate numerous muscle-fibres which pass through *b. c.*[1] to the anterior wall of the proboscis. The internal opening of the right proboscis-pore (*p. p.*) is seen, and the whole extent of the central nervous system (*c. n. s.*).

In fig. 46, the right edge of the proboscis-stalk is cut, and the collar-cavity (*b. c.*[3]) is continuous from the arm-base (*a. b.*), dorsally, round the right side of the mouth, to the operculum, ventrally. The operculum is clearly a derivative of the anterior edge of the collar, while the collar-canal (*c. c.*) occupies a ventro-lateral recess of the second body-cavity, immediately in front of the gill-slit. As the pharynx no longer reaches the dorsal body-wall, the second and third body-cavities are separated by a thin septum (*s.* $^2/_3$).

1) It will of course be noticed that the arms shewn in the reconstructions, figs. 22, 25, are those of the right side.
2) It will be convenient to indicate this as "septum $^1/_2$", and that between the second and third cavities as "septum $^2/_3$".

In fig. 47, the right arms (those shewn in the reconstructions figs. 22, 25) are becoming apparent. While the preceding section (fig. 46) has no trace of food-grooves, the present section shews the commencement of the grooves (*R.* 1, *R.* 2) of the first two arms of the right side.

The structure of the remaining sections (figs. 48—53) will be clear with the aid of the reconstructions, figs. 22 and 25. It will be noticed that the food-grooves 2—5 successively make their appearance; and it is clear that as these sections are transverse to the grooves, the fact that the latter are not traceable to the mouth indicates that they die away in approaching that aperture. It will be seen that each of the arms passes directly outwards for some little distance from its base, as is implied by the fact that near the middle line of the animal the arms are cut transversely. This position corresponds closely with that in which the arms are developed in the bud (cf. fig. 32); and although the arms are of course able to place themselves in a great variety of attitudes, they happen to be in what may be regarded as their normal position on the right side of this individual. After passing outwards for some distance, they for the most part turn dorsally, as shewn for *R.* 1 in figs. 52, 53, and for *R.* 1 and *R.* 2 in fig. 22. They may at the same time be twisted about their own longitudinal axis, as indicated for *R.* 5 in figs. 25 and 22.

Tracing the arms from the outer side towards the mouth it will be seen that the food-grooves fade away as they pass into a tunnel-like space bounded by the anterior wall of the arm-base, the operculum and the posterior wall of the proboscis. This tunnel curves round the proboscis-stalk until it leads to the mouth.

The figures further demonstrate the existence of the lateral lobe of the operculum, which projects a considerable distance externally to the point where the arms become free. Fig. 51 shews the level at which this lateral lobe begins to be free. It is indeed still connected with the base of the fifth arm, but its cavity is disconnected from that of the arm, since the section merely cuts the marginal epidermis of the part of the operculum which immediately adjoins the arm. In the more external sections (figs. 52 and 53) the operculum is quite separate from the arms. One further point may be noticed in this series of sections. The collar-canal (*c. c.*) is seen to be a short tube which opens into the collar-cavity at the end situated nearer the middle line of the collar, and to the exterior at its more external end. By the time the external opening is reached, the collar-cavity itself has disappeared; or, in other words, the collar-canal occupies a lateral recess of the collar-cavity.

The number of arms, in this as in other species of *Cephalodiscus*, appears to be in the main constant for each species. It is sometimes, however, no easy task to count the arms in sections which are not favourably orientated, while results based on entire preparations are uncertain. In one series of sections of *C. gracilis*, I have convinced myself of the existence of six arms on one side, instead of the normal five; while in one case of *C. dodecalophus*, I have only been able to count five arms on one side. It would almost be expected that some variation would occur in these respects. The variation might well make its appearance in the bud, by the greater or smaller amount of subdivision of the free dorsal edge of the collar.

C. dodecalophus.

The complicated arrangement of the arms in this species can be explained by comparison with *C. gracilis*. I defer considering the account which MASTERMAN (**98**, 2, p. 521) has given of this subject until I have described the arms of *C. levinseni*.

The fundamental arrangement of the arms of *Cephalodiscus* is most easily seen in the buds, and is shewn in MASTERMAN's figs. 25, 24 and 27 (Pl. II) of the paper just referred to, or in my own figures (Pl. III, figs. 32, 30; Pl. I, fig. 4) of the buds of *C. gracilis*. The arms are developed as a simple linear series of outgrowths, at the sides of the central nervous system, from the dorsal extremity of the collar. The most anterior arm is developed first, and the others in regular order from before backwards. This arrangement is but little disturbed in the adult *C. gracilis* (figs. 52, 53).

Figs. 151—141 (Pl. XII) represent every second section of a series of *C. dodecalophus*, and readily admit of comparison with figs. 43—53 of *C. gracilis*. The plane of the sections may be described as obliquely sagittal, the first section (fig. 151, which is more highly magnified than the others) passing through practically the middle line of the proboscis, at the front end of the central nervous system, and through the extreme outer edge of the collar-canal on the ventral side. As both sides of the metasome are, however, cut there was probably some rotation of the anterior part of the body in the neck-region.

Fig. 151 shews the external opening of the left proboscis-pore (*p. p. l.*), the anterior dorsal horn of the left collar-cavity (*b. c.*^{2} *a.*), the tip of the notochord (*nch.*), and the dorsal collar-mesentery, connecting the notochord with the central nervous system. The collar-cavity (*b. c.*^{2} *r.*) is cut along nearly its entire length, the section passing to the right of the mouth. At the ventral end of the cavity is seen the outer edge of the collar-canal (*c. c. e.*), which lies in a recess of this region of the collar-cavity. Immediately behind the collar-pore is the strong nerve-tract or lateral nerve (*l. n.*) passing from the central nervous system (*c. n. s.*) to the stalk.

The succeeding figures represent sections lying further to the right than the one which has just been described. Fig. 150 has nearly reached the superficial groove which separates the collar from the metasome. The lateral nerve is seen passing from the central nervous system, behind the collar-cavity, to reach the ventral surface. The extreme tip of the notochord (*nch.*) is cut by this section; immediately in front of it being the pericardium (*per.*), the internal opening of the left proboscis-pore (*p. p. l.*) and the anterior end of the left collar-cavity (*b. c.*^{2} *a.*).

Fig. 149 shews the last of the connexion between the collar and the metasome. The position of the collar-pore in the preceding sections is now overhung by a lateral lobe of the operculum (*op. r.*), developed as in *C. gracilis*, its morphologically external wall being cut tangentially in this section.

In fig. 148, the lateral lobe of the operculum is cut so as to expose most of its cavity, which is separated by a ridge of the basement-membrane (cf. fig. 153, *b. m.*) from the rest of the collar-cavity. The inner edge of the right proboscis-pore (*p. p. r.*) is cut tangentially.

In fig. 147, the lateral lobe of the operculum is separated from the arm-base (*a. b.*), which is the more dorsal part of the collar-edge. The external opening of the right proboscis-pore is

seen, immediately dorsally to the base of the first arm (*R.* 1). The dorsal horn of the right collar-cavity (*b. c.*^{2} *a.*) projects into the first body-cavity, the septum $^1/_2$ in this region affording origin to radiating muscles which traverse *b. c.*^{1} to reach the anterior wall of the proboscis.

Fig. 146 cuts the animal at a level where the collar is just losing its connexion with the proboscis. The first arm (*R.* 1) is becoming more distinct, and the food-groove of *R.* 2 is obvious. The second and third arms are indicated dorsally by small triangular ridges. It should be specially noticed that there is no trace of the food-grooves of the arms 3—5; and the direct continuity of the food-grooves with the mouth, described by MASTERMAN, appears thereby negatived.

In the succeeding sections (figs. 145—141) the arms become progressively more distinct, their food-grooves appearing as the series of sections is traced outwards, and their angular dorsal surfaces becoming increasingly prominent. The lateral lobe of the operculum comes to an end in fig. 142, and in the last section shewn (fig. 141) it is no longer seen, while the arms have become completely separated from one another. It will further be noticed that the complete separation of the arms from one another is preceded by the ingrowth of a ridge of basement-membrane, so that the cavities of the arms become individually distinct before their epidermic walls are completed.

C. levinseni.

The arms of this species are six in number on each side, and their general arrangement resembles that found in *C. dodecalophus*. Their structure may be illustrated by means of the series of frontal sections shewn in Pl. X, figs. 111—118. The histological preservation of the specimens not being very good, the nerve-layer is not shewn except in the region of the central nervous system and of the strong commissural or "lateral" nerves to the stalk. But there is no reason to suppose that it differs essentially from that of *C. dodecalophus*.

Fig. 112 passes through both proboscis-pores (*p. p.*), as well as through the pericardium (*per.*) and the anterior horns of the collar-cavities (*b. c.*^{2} *a.*). The first three arms of the right side (*R.* 1—3) have not yet separated from the arm-base; while on the left side, the arms were lying in such a position that five of them are cut separately.

Fig. 113, immediately behind the proboscis-pores, shews both the first arms originating from the anterior dorsal extremities of the collar. The six arms of the left side are seen, *L.* 1 and *L.* 2 being connected with one another by their epidermis, although the section passes dorsally to the level at which their body-cavities become continuous. On the right side is seen the common base of the first three arms, posterior to the region where their cavities become separate. The tip of the notochord (*nch.*), encircled by the posterior end of the pericardium (*per.*), occurs immediately below the central nervous system (*c. n. s.*). The proboscis-stalk is separating from the buccal disc.

Fig. 114—117 are sufficiently explained by the lettering, but it will be noticed that in passing backwards, the arms first become connected by their epidermis and that the complete union of their cavities is preceded, as in *C. dodecalophus*, by the appearance of a ridge of basement-membrane which may be cut in such a way as to form a complete septum across the

collar-cavity of this region. The septum has, however, a free internal edge (cf. Pl. XI, fig. 140), so that the arm-cavities become successively continuous with the general collar-cavity.

The plane of the sections is not well suited to demonstrate the relation between the arms and the operculum; but it is sufficiently obvious that the base of the operculum is cut immediately after the disappearance of the sixth arm on either side (figs. 118, 119), and that in fact it is the last arm on each side which becomes continuous with the operculum. It will be remembered that the operculum is an exceedingly mobile organ, which can place itself in a great variety of positions. In this particular specimen the left side of the operculum is in the main standing at right angles to the proboscis-stalk, but with some forward direction. On the right side, the operculum is directed backwards over the region of the collar-pore and gill-slit. It thus results that in tracing the series backwards, the operculum appears first on the left side (figs. 116—118); it is later cut tangentially on the same side (figs. 119—121), although the sections are complicated by the presence of several folds in the organ; while on the right side (figs. 118—123) the sections of the operculum have a simple character, owing to the fact that it is hanging ventrally and backwards from the mouth.

The beginning of the right half of the operculum is indicated in fig. 118 by a ridge of basement-membrane (*b. m.*) which projects into the right collar-cavity. This ridge resembles those which form the commencements of the arm-cavities, and like them has a free internal edge. The separation of the operculum from the rest of the collar is seen, on the left side, in fig. 119 by projections of the basement-membrane (*b. m.*) developed from both the dorsal and the ventral sides of the collar-cavity. The basement-membrane which lines the operculum is quite thin, which is in marked contrast with the condition found in the main part of the collar-cavity and in the arm-bases (figs. 119—122). It may be presumed that the basement-membrane has a supporting value, and that its great development in the arm-bases is connected with the fact that these parts are relatively stiff compared with the mobile operculum.

The later sections figured (figs. 120—124) shew the collar-cavities passing at the sides of the mouth and finally uniting on the ventral side of that aperture (fig. 122). The collar-canals (figs. 121, 122) are situated in the ventral end of that part of the collar-cavity which is continued into the arm-base.

The left series of arms shewn in figs. 113—117 has an extremely characteristic arrangement, which can also be made out on the right side, although these arms are lying in a position which is not quite so favourable for demonstrating their real relations.

It will be seen from fig. 113 that while the arms *L.* 1 and *L.* 2 have their food-grooves facing the proboscis, *L.* 3 faces directly outwards, and *L.* 4—6 face away from the proboscis. A similar arrangement has been described by Masterman (**97**, 2, p. 346, Pl. XXVI, figs. 32—36; **98**, 2, p. 521, Pl. IV, fig. 68) in *C. dodecalophus*, the diagrammatic figures shewing three of the arms facing the proboscis and the other three with their backs to the proboscis. Now while the account given in the earlier account is perfectly correct, in the second paper referred to Masterman inverts the numbering, and moreover describes a process of rotation of the arms which is supposed to bring them into the position shewn in his figure. No mention is made of the discrepancy between the two accounts, and I am unable to explain why Masterman

discarded his first and correct description for one which does not agree with the facts. The point is really one of importance; as without a proper understanding of the order of the arms it is impossible to grasp the manner in which the food must pass to the mouth; and moreover, the possibility of comparing the collar-region of *Cephalodiscus* with that of other animals clearly depends on an accurate knowledge of its structure. As I cannot accept MASTERMAN's account, it follows that I do not agree with his theoretical conclusions on the subject.

As no two individuals of *Cephalodiscus* have their arms in identically the same position, it is clear that the arms can be moved at the will of the animal into an indefinite number of positions. I do not therefore assert that MASTERMAN's second diagram represents an impossible arrangement, though I do not think it would be easy to find it. But the whole significance of a diagram of this kind depends on shewing the relations of the arms to one another at their bases, where the arrangement is invariable, except so far as it may be slightly modified by muscular contractions. Any such diagram of the bases of the arms must accordingly shew the first arm in the position of MASTERMAN's sixth (**98**, 2); and, vice versa, the sixth in the position of his first. It is perfectly certain that the arm which I call the first originates from the front end of the dorsal part of the collar, in the immediate neighbourhood of the proboscis-pores, and with its food-groove facing the flattened part of the proboscis. This is shewn, for *C. levinseni*, in figs. 112, 113 and for *C. dodecalophus*, in figs. 148—143. It may thus be stated that in both these species the arms are arranged, as seen in frontal sections, as a series of *V*-like structures, their dorsal angles radiating to a common point, and their food-grooves being disposed round the periphery of a circle. The difficulty of getting sections which shew this arrangement quite diagrammatically depends on the facts (I) that the arms may be directed in any direction — forwards, backwards, outwards or inwards — as soon as they have become free, and this movement may be associated with rotation round their longitudinal axes; (II) that the arm-bases are not all in a single plane. The first difficulty is most easily overcome by examining sections of *C. levinseni*, in which the arms are very commonly arranged parallel with one another in a bundle which is directed straight forwards. The second difficulty cannot be so easily surmounted. The arm-bases of each side in reality follow a spiral line, commencing close to the proboscis-pore, and passing outwards and then dorsally, the end of the spiral reaching the posterior end of the central nervous system. In *C. gracilis* (fig. 25) the arm-bases follow a comparatively simple line, although even in this species no two individuals have their arms in the same position. The arrangement in *C. levinseni* can be understood by imagining the number of arms in *C. gracilis* increased by one, and by supposing the last arm of the series to be carried a considerable distance inwards, or towards the middle line of the animal.

I have attempted to shew, in a diagrammatic figure (Pl. XII, fig. 158), a posterior view of the arm-bases of the left side of *C. levinseni*, based on the frontal sections which have already been described. A similar dorsal view of the arm-bases and of the operculum is given in fig. 160; while fig. 159 is what I believe to be a fair diagrammatic representation of the free edge of the collar. In this last figure, in which the proboscis-stalk is supposed to have been cut through, and the anterior end removed, it has been necessary to exaggerate the size

of the operculum, in order to shew its relations to the food-grooves of the arms. It must be realized that the food-groove of the sixth arm passes towards the axis of the projected spiral, at a deeper level than that shewn in the figure. The free edge of the operculum (which is continuous with the sixth arm) is thus represented as starting too near the dorsal middle line. It will further be apparent from the actual frontal sections that the cavities of all the arms pass into the general collar-cavity which is situated at a lower level than (in reality, posterior to) the portion of body-wall which is formed by the continuous dorsal surfaces of the arms in the diagram.

Although fig. 159 is thus not an exact representation of the collar of *C. levinseni*, it is, I believe, correct as a diagram. The possible relations of the arrangement here shewn with the lophophore of *Phoronis* will be considered later.

C. sibogae.

In the neuters of this species the relations of the collar resemble those already described in the other species. There are, however, only four pairs of arms (Pl. VIII, fig. 93; Pl. IX, fig. 97), while the operculum (Pl. IV, fig. 40; Pl. VII, fig. 78; *op.*) is very large. The collar is moreover provided with specially strong muscles, the relatively high development of the muscular system being marked in both the collar and the metasome of this species.

The peculiar features of the male will be considered in Section XV. The remarkable arms (Pl. VII, figs. 72—76, 79; Pl. IX, figs. 95, 96, 99) are only two in number. They are circular in section (fig. 79) except close to their base, where a vestige of a food-groove persists, leading by means of a food-channel (fig. 79, *f.c.r.*, *f.c.l.*) to the mouth, which is shewn in fig. 95. The male has no operculum.

End-bulbs.

Each arm in *C. dodecalophus* terminates, as is well known, in a globular end-bulb, which possesses remarkable refringent vesicles. These structures were described by M'Intosh (**87**, p. 11) as glandular in nature. Masterman (**97**, 2, p. 344) suggested that they are compound eyes, a view which he subsequently discarded (**03**, p. 725). Cole (**99**) regards them as rhabdite-producing organs.

I have myself no evidence which decides the function of the end-bulbs, although I refer to the subject again in describing the males of *C. sibogae* (Sect. XV), in which refringent vesicles are present in extraordinary numbers along the whole course of the arms. The bulbs are conspicuous structures in the buds of *C. gracilis*, where they seem to be invariably present at the ends of the arms of the first two pairs, while they may also occur on the third arms. I have no evidence that they are found on the fourth and fifth arms, while it seems probable that the vesicles may completely disappear from all the arms of some of the adult specimens, in this species. I have not found distinct end-bulbs or refringent vesicles either in the neuter individuals of *C. sibogae* or in *C. levinseni*.

Some further information with regard to the arms of *Cephalodiscus* is given in describing the muscular system (Sect. XII), while the tentacles are alluded to under the heading of the vascular system (Sect. XIV).

The collar cavity and its contents.

The collar-cavity consists of a pair of coelomic sacs which transversely encircle the oral region of the animal. The dorsal mesentery persists throughout, while the ventral mesentery is only represented in that region which lies posteriorly to the origin of the operculum (Pl. IX, fig. 107; Pl. X, figs. 123, 124, *v. mes.*^{2}). In front of this region the right and left cavities become continuous by the disappearance of the mesentery (fig. 122), a result which probably allows the operculum to behave as a single organ; — which it could hardly do if it were subdivided by a median septum.

A sagittal section of *C. dodecalophus* (Pl. IV, fig. 42) shews a considerable extent of collar-cavity on the dorsal side of the body, and a very small portion on the ventral side. The operculum is short in the middle ventral line, and a section in this region accordingly shews the minimum amount of collar-cavity which it is possible to see. A median sagittal section should theoretically include the dorsal mesentery of the collar; but that membrane is extremely thin, and moreover it seldoms lies completely in one plane (cf. Pl. XI, fig. 137). Fig. 42 thus shews one of the collar-cavities, instead of the mesentery, on the dorsal side.

While the posterior boundary of the collar-cavity lies in a plane which is nearly transverse to the first part of the alimentary canal, the anterior boundary has a more complicated course. In the position which has been assumed by the individual shewn in fig. 42, the dorsal part of the collar-cavity is elongated in a direction which makes rather more than a right angle with the posterior wall. In other individuals, in which the neck is more sharply bent (as in figs. 150, 151), the dorsal part of the collar-cavity may lie almost in the same straight line with the transverse part. The dorsal part of the collar-cavity, with which the arms are connected, is however, so arranged as to overlie the proboscis-cavity on its dorsal side. A frontal section of the buccal disc thus shews three cavities (Pl. XII, fig. 152); the two collar-cavities (*b. c.*^{2}) separated by their dorsal mesentery (*mes.*^{2}), and the unpaired proboscis-cavity, which occupies the anterior part of the section. Along the septum $^1/_2$ thus constituted runs the notochord (*nch.*) supported medianly by the dorsal mesentery of the collar, and laterally by the two halves of the septum $^1/_2$.

Masterman (**03**, p. 717) has stated that there is a difference between *Cephalodiscus* and Balanoglossus in the relations of the notochord, which "lies in its primitive position in the "collar, and is in no way produced into the pre-oral cavity. It is a backward ventral extension "of the buccal shield which makes the subneural gland [= notochord] lie in front of the mouth, — "not, as in Balanoglossus, a forward median extension of the subneural gland into the "pre-oral cavity". I confess that I am unable to appreciate this distinction. The notochord in Balanoglossus may indeed project further into the anterior body-cavity than in *Cephalodiscus*, but I can see no morphological difference of importance between the condition shewn in the figure on p. 23 and that which obtains in Balanoglossus. It is no doubt true that the notochord is in relation with the two halves of the collar-cavity along practically its whole length

(cf. Pl. XI, fig. 138), but the relations which it eventually acquires with the anterior body-cavity and the pericardium (Pl. XIII, fig. 181) do not differ essentially from those found in the Enteropneusta. This is indeed admitted by MASTERMAN in a later part of his paper (p. 722).

Sagittal sections of *C. levinseni* (Pl. IV, figs. 34—36) and *C. gracilis* (Pl. IV, fig. 37; Pl. V, figs. 43—51) shew an essentially similar condition; but in both these species the ventral part of the collar-cavity is better developed than in *C. dodecalophus*, although in all three cases the operculum is lower in the middle line than it is more laterally.

The relations of the dorsal collar-region are best illustrated by means of sections transverse to the long axis of the zooid. The series of sections of *C. levinseni* shewn in Pl. X are from an individual whose proboscis-stalk was turned more dorsally than in Pl. IV, fig. 34, so that their direction, as compared with that figure would be represented by a line joining the posterior end of the central nervous system to the tip of the operculum.

Fig. 117, through the base of the notochord, thus cuts the posterior part of the proboscis-stalk in such a way as to shew no part of the proboscis-cavity (cf. fig. 33). The collar-cavities occupy the whole of the proboscis-stalk, extending laterally into the arms and separated medianly by their dorsal mesentery, at the ventral end of which lies the notochord.

In fig. 115, which is further forward, two portions of the proboscis-cavity (*b. c.*[1]) appear on the ventral side of the collar-cavities, one of than in a detached portion of the proboscis-stalk, due to a fold, doubtless caused by muscular contraction.

In fig. 114, this fold has opened into the main part of *b. c.*[1], and the notochord is now supported by three membranes, in the way that has been described above. In fig. 113, the ventral body-wall of the proboscis-stalk is about to become continuous with the buccal disc. The section cuts the tip of the notochord, the lumen of which is here considerably dilated. The notochord has moved up the collar-mesentery, so as practically to reach the central nervous system, as described by MASTERMAN (**03**), and it is overlapped by the posterior end of the pericardium (*per.*), which separates the two collar-cavities from one another so that they are no longer divided by a simple mesentery (see also Pl. XI, fig. 138). The collar-cavities now rapidly diminish in passing forwards. Immediately in front of the bases of the first arms (fig. 112) they are left as a pair of small cavities, the anterior dorsal horns of the collar-cavity (*b. c.*[2] *a.*), distant from one another, and separated from the pericardium by the proboscis-pores (*p. p.*), just in front of which the collar-cavities terminate.

The whole of this region of the collar-cavity is lined by a strong basement-membrane, which in addition to the stiffening function which it doubtless possesses gives origin to muscles that traverse the proboscis-cavity. It seems to me probable that the anterior horns of the collar-cavities may be functionally related with the proboscis-pores, closing them by the contraction of the muscles which originate from them, aided, it may be, by a dilatation of the anterior horns of the collar-cavities by the forcing of fluid into them from the rest of the cavity. It is, however, clear that the horns are most important structures in prolonging the origin of the system of muscles (Pl. XII, figs. 147—149) which radiate through the proboscis-cavity.

The relations of the anterior horns of the collar-cavities described in *C. levinseni* are also found in the other species, and have already been described, in *C. dodecalophus*, by MASTERMAN (**03**).

Tracing the sections of *C. levinseni* ventrally it will be seen that the collar-cavities become separated from one another by the diverticulum of the pharynx (Pl. X, fig. 118) and begin to pass round the alimentary canal to the ventral side. The dorsal projection of the metasome (*met.*) containing the oviducts appears behind the collar-region, and the two collar-cavities become more and more separated from one another dorsally by the third body-cavities (figs. 118—124, *b.c.*[3]). The operculum originates ventro-laterally from the collar (figs. 118—122), as has already been described; and the direct continuations of the dorsal parts of the collar-cavities, specially connected, as has been shewn above, with the arm-bases, terminate ventrally in the regions containing the collar-canals (fig. 122, *c.c.*). The more anterior portions of the cavities (cf. Pl. XII, fig. 151) are, however, continued round the ventral side of the alimentary canal, where they become completely confluent (fig. 122). As soon as the base of the operculum has been passed, a ventral collar-mesentery makes its appearance (fig. 123). The collar-cavities may be seen, in several sections further, on the ventral side of the third body-cavities (fig. 124), the reason for which will at once be apparent from an inspection of the sagittal section (Pl. IV, fig. 34). The ventral mesentery persists to the posterior end of the collar-region (Pl. IX, fig. 107).

The relations of the collar-cavities in *C. dodecalophus* differ in no important respects from those above described. This will be clear from an inspection of figs. 151—146 (see p. 34); but attention may specially be called to fig. 151, which shews that the collar-canal occupies the ventral end of the part of the cavity which encircles the alimentary canal, and is a direct continuation of the cavity of the arm-base.

The same arrangement is shewn, for *C. gracilis*, in the series of obliquely sagittal sections, Pl. V, figs. 43—51, and in the frontal sections, Pl. VI, figs. 63—68; and, for neuter individuals of *C. sibogae*, in Pl. XIII, figs. 182—185 (young), Pl. VIII, fig. 93 and Pl. VII, figs. 77, 78.

Collar-pores or Collar-canals.

There are no organs in *Cephalodiscus* which have given me more trouble than the collar-canals, and this in consequence of the difficulty of forming a reasonable theory as to their mode of action. The general facts are perfectly clear. Each collar-pore or collar-canal is an ovoid body which lies with its long axis more or less transverse to that of the body (Pl. XI, fig. 131, *c.c.*). On the median side, the canal opens by a large aperture into the collar-cavity. On the outer side it opens by an even larger aperture (*c.c.e.*) to the exterior. It follows from this disposition of the organ that both apertures may be cut in a single section which passes either in a transverse plane (fig. 131) or in a frontal plane (Pl. X, fig. 121); and that a section which passes transversely to the long axis of the organ must have a more or less sagittal direction (Pl. XI, fig. 140). But with varying states of contraction of the collar, these relations may be somewhat distorted.

The collar-canal lies at the ventral end of that section of the collar-cavity which is directly continuous with the arm-base (Pl. XII, fig. 151; Pl. V, figs. 46—49; Pl. XI, fig. 140). Its ventral wall is in immediate contact with the dorsal wall of the gill-slit (figs. 46, 131, 140), but it rests partly on the septum which divides the collar-cavity from the trunk-cavity (figs. 49, 140, 155). This wall is composed of a high epithelium with numerous nuclei, implying narrow,

closely packed cells, and it bears long cilia or flagella (fig. 140). In either a transverse or a sagittal section this high epithelium has a characteristic crescentic form.

The dorsal wall of the canal is formed of a much thinner epithelium (figs. 131, 140; Pl. V, figs. 46—50). It may either be convex towards the lumen of the canal, and therefore more or less parallel to the ventral wall (figs. 49, 131), or it may be flat (Pl. XIII, fig. 185), or it may be concave towards the lumen (figs. 101, 140). The latter condition gives the largest size to the cavity, and the collar-canal may be said to be dilated when it is in this condition. It appears obvious that the dorsal thin wall is capable of a considerable amount of movement, and it may be presumed that this mobility is of physiological importance.

It is further obvious that the longitudinal muscles of the trunk end in the immediate neighbourhood of the collar-canal (fig. 140, 77, 93); that a specially strong band of collar-muscles originates in much the same position (figs. 131, 77, 93, *or. m.*); and that the anterior flexible wall of the canal is in the closest connexion with a tissue (figs. 131, 140, 121, 122, *x*.) which appears to consist of a series of radiating lamellae.

The above facts can easily be verified in any female or neuter zooid (*C. sibogae*), although in the males of *C. sibogae* the collar-canals are so small that the details of their structure have not been made out.

It follows from the observations of Spengel (**93**, p. 475) that the collar-canals of Balanoglossus are of special importance in taking water from the outside into the collar-cavities, and so maintaining the collar as a whole in a proper state of turgidity. I think it cannot be doubted that the same is true of *Cephalodiscus*. The whole mechanism of the collar appears to depend on the proper maintenance of this condition. The movements of the arms and of the operculum are alike dependent on it. The arms in particular are provided with strong longitudinal muscles, by which they can be contracted; but for their elongation and for that of the tentacles, one must look to the fluid pressure of the contents of the collar-cavities. The mechanism is probably identical with that of the tube-feet of an Echinoderm, and the resemblance is made all the more striking by the fact that most parts of the collar-coelom are traversed by short fibres which connect the opposite walls (Pl. X, fig. 122) as in the case of the ambulacral canals of a Crinoid, for instance. When it is remembered that MacBride (**96**, p. 396) has given reasons for regarding the hydrocoel system of an Echinoderm as actually homologous with the left collar-cavity of Balanoglossus the similarity between these cavities in *Cephalodiscus* and the ambulacral vessels of an Echinoderm becomes all the more noteworthy.

A strong contraction of the longitudinal muscles of the arms must have the effect of forcing their fluid into other parts of the collar; and as there are no spaces which appear to have the function of reservoirs, I think it follows that fluid must leave the collar by way of the collar-pores. During the extension of the arms, on the contrary, fluid must be supposed to be taken in by the collar-pores, which thus act now as exhalant and now as inhalant apertures. How are these varying currents controlled? The strong flagella of the ventral epithelium of the collar-canals are no doubt of special importance in the process; but the mode of ending of some of the strongest muscles of the body in the immediate vicinity of the pores is significant, and it appears to me that it may imply something in the nature of a pumping action.

A mechanism of this sort would require some power of closing either one or both of the apertures of each canal, as occasion requires. The condition in which the canals are left in preserved specimens is, however, usually one in which both external and internal apertures are widely open.

The consideration of these questions must be preceded by a more careful study of the collar-canals themselves.

The external aperture of a collar-canal (*c. c. e.*) is seen in Pl. III, fig. 25, which is drawn from a plasticine reconstruction of the sections belonging to the sagittal series shewn in Pl. V. The external part of the opercular flap is cut away on the right side, and immediately below this part the collar-pore appears as a projection of the body-wall in the form of half of a shallow cup. Below the collar-pore is seen the aperture of the corresponding gill-slit (*g. s. r.*). Figs. 50—46 shew consecutive sagittal sections of this collar-canal. It appears from these sections that the external aperture of the canal is everywhere overhung by the base of the operculum, and the arrangement suggests that this structure when reflected towards the stalk of the animal, might be used for closing the collar-pore. There is also clear evidence of a tissue passing from the thin dorsal wall of the collar-canal to the base of the epidermis of the oral side of the operculum. If this tissue were muscular the collar-canal would appear to be provided with a dilating mechanism.

But in most other cases I have not been able to demonstrate any connexion between these supposed dilator fibres, which I will term the "problematical tissue" of the collar-canals, and the oral epidermis of the operculum.

Two sets of muscles are, however, intimately associated with the collar-canals. The first of these are the great antero-ventral muscles of the body, continuous ventrally with those of the stalk. These muscles (Pl. X, figs. 125, *ms.*) divide into two masses when they reach the level of the ventral border of the collar (fig. 124), the fibres becoming fewer in number; and they diverge outwards as they cross the gill-slits on their anterior side (fig. 123), finally disappearing when they reach the trunco-collar [1]) septum in the neighbourhood of the inner openings of the collar-canals. These antero-ventral horns of the third body-cavities (*b. c*^{3}. *a.*) are seen in longitudinal section in Pl. IV, fig. 41 (*C. dodecalophus*) and in Pl. IV, fig. 36 (*C. levinseni*). They are essentially alike in all the species which I have examined.

The second set of muscles are the strong oral muscles (*or. m.*) which traverse the collar in a longitudinal direction. These muscles (Pl. IV, fig. 41; Pl. V, fig. 45; Pl. VIII, fig. 93) originate from the trunco-collar septum close to the insertion of the muscles contained in the anterior horns of the third body-cavity, and pass dorsally round the sides of the mouth, ending in septum $^1/_2$ opposite the point of origin of the radiating muscles which pass freely through the cavity of the proboscis.

Since the ventral wall of the collar-canal is firmly attached to the septum with which these two sets of muscles are connected, it would appear that contraction of the muscles must have some effect on the collar-canal. This organ has a perfectly characteristic relation to the

1) I borrow this expression from DE SELYS LONGCHAMPS (04).

gill-slit, on the dorsal side of which it rests. Pl. XI, fig. 131 will shew, however, that the contact between the two organs only concerns the middle of the ventral wall of the collar-canal, the inner part of the wall resting on that portion of the trunco-collar septum in which the muscles of the metasome end, while the outer part is confluent with the external part of the septum. This relation is further illustrated by Pl. XII, figs. 156, 155. If a tracing be made of fig. 155 and if it be superposed on fig. 156, it will be seen that the long axis of the collar-canal crosses the gill-slit at right angles; and the consideration of the figures which have been referred to thus suggests the idea that the wall of the gill-slit in fact forms a fulcrum on which the collar-canal moves. If this conclusion be correct, it would appear that the contraction of the muscles passing from the stalk to the inner and anterior wall of the collar-canal must depress that end of the organ, and elevate its outer end. But the contraction of the longitudinal muscles of the trunk presumably increases the fluid pressure of the contents of the third body-cavity. This increase would probably react mainly on the outer end of the collar-canal, partly because the area of the septum exposed to the pressure is here greater than at the internal end, and partly because the anterior horns of the third body-cavity are for the most part filled with muscle. The pressure-effect would thus act in the same direction as the direct effect of the contraction, and the projecting ventral lip of the external aperture of the collar-canal would move in a dorsal direction. A collar-canal in this condition is seen in Pl. III, fig. 24, the external opening being here nearly closed, instead of having the widely open condition shewn in Pl. XI, fig. 131.

When the collar-canal has assumed the position indicated in fig. 24, it seems natural to suppose that the contraction of the strong oral muscle which traverses the collar-cavity will restore the collar-canal to its former position by elevating the inner end of the organ, since the origin of those fibres is immediately adjacent to the insertion of the metasomatic muscles.

I am inclined to believe that the external opening of the collar-canal can be closed, partly by the contraction of the musculature of the metasome, and partly by the movements of the operculum. Even when the free edge of that organ is directed forwards, the operculum might still be effective in helping to close the collar-pore, as is indicated by fig. 24, where a sharp bend of the operculum is almost in contact with the ventral lip of the collar-pore. If the collar-pores were closed, the arms, tentacles and other parts of the collar would presumably be in full working order, since their body-cavities would form a closed system, and contraction of any of the muscles would be capable of producing an effect on the fluid pressure of the collar-coelom. Should any sudden retraction of the arms be required this could be effected by the contraction of their longitudinal muscles, the fluid meanwhile escaping through the widely open collar-pores.

The "problematical tissue" (x.) of the collar-pores offers more serious difficulties. It is in the first place necessary to decide whether the tissue is muscular or is a modification of the basement-membrane, of skeletal or elastic properties. The evidence of stains seems to be unequivocal on this point. The tissue stains like the muscles. The clearest evidence is afforded by specimens stained with haematoxylin and Orange G; and in these, while the basement-membrane has taken up the haematoxylin colour, the problematical tissue, like the muscles of

the stalk and other parts, is brilliantly orange in colour. Although I think that the evidence of the stains must be relied on, there are two facts which make it difficult to interpret the tissue as muscular in nature. These are (*a*) the form of the elements of which the tissue is composed, and (*b*) the mode of connexion of the tissue with adjacent parts.

With regard to (*a*) it must be pointed out that the tissue appears to be composed of oval lamellae, and not of typical muscle-fibres. A sagittal section (fig. 140) or a frontal section (figs. 120, 121) will give the impression of muscle-fibres cut longitudinally. It is obvious that if a linear organ appears as a line in sections cut in two planes at right angles to one another, a section in a plane at right angles to both the others will shew it as a point. I have been unable to obtain any sections in which the elements of the problematical tissue appear as a series of points; and, on the contrary, a transverse section (fig. 131) gives the impression that the organ is composed of a series of oval lamellae. These stain in precisely the same way as the typical muscle-fibres of the body, and a certain number of nuclei can usually be made out along their free coelomic borders. This form of the elements of the tissue precludes the possibility that the problematical tissue consists of a mass of solenocytes; and Mr E. S. Goodrich, who was kind enough to look at one of my preparations, expressed the opinion that the tissue cannot be explained in that way.

With regard to (*b*), it may be noticed that the elements of the tissue are not so obviously provided with an origin and an insertion as would be expected on the hypothesis that they are muscular. This will be seen in such cases as fig. 140 where the lamellae have a free coelomic border, a condition which is also seen in figs. 120, 121, 131.

If the tissue really consists of dilator fibres, a function which is suggested by the specially wide lumen of the collar-canal seen in fig. 140, it would be expected that the ends of the fibres would originate from the walls of the collar-cavity. In view of the strong development of the tissue in question it is clear that its muscular nature cannot be regarded as proved unless a sufficient origin can be detected.

In view of these considerations, and of the fact that figs. 47—49 seem to shew that the elements of the problematical tissue are connected with the inner wall of the oral side of the operculum, I have endeavoured to find evidence that the origin of the fibres has been torn away from the body-wall, owing to imperfect preservation. Such a view is, on *a priori* grounds, not improbable, as the elements appear to be very powerful, and might have undergone contraction, during the death of the zooids, sufficient to tear them away from their origin. Fig. 131 certainly indicates that the coelomic epithelium of the dorsal side of the collar-cavity has been torn away from its basement-membrane; but even in this case, I cannot satisfy myself that the oval lamellae can have originated from that wall of the cavity. The probability that the relations of the tissue, in the preserved material, are not essentially different from those found during life is increased by the considerations (*a*) that rupture of the connexions of the tissue might be expected to occur, in some cases at least, at the end which is inserted into the delicate dorsal wall of the collar-canal; and no such rupture is observed; (*b*) that the undoubted muscles of the animal are seldom found to be torn away, at either end, from the basement-membrane to which they are severally related.

I am thus led to the conclusion that the problematical tissue must be interpreted as it stands, without the aid of any hypothesis to the effect that rupture has taken place; and it remains to consider further the evidence afforded by the sections. Sagittal sections (fig. 140) shew that the lamellae stand more or less at right angles to the wall of the collar-canal; or, in other words, that they radiate from its lumen. Frontal sections (fig. 121) shew that they originate from the lateral body-wall of the collar, an arrangement which is also seen in transverse sections (fig. 131) or in the reconstruction shewn in fig. 24. Although it would not be difficult to imagine that the lamellae had been torn away from the basement-membrane covering the pharynx in figs. 120, 121, the fact that the oral muscle (*or. m.*) of the collar intervenes between the pharynx and the problematical tissue makes it impossible to suppose that this tissue was connected with the pharyngeal wall along the whole of what appears as its free border in figs. 120, 121.

The relations of the problematical tissue can thus be expressed by saying that each of the lamellae of which it is composed is connected, along about half of its circumference (see fig. 131) with the thin dorsal wall of the collar-canal and with the external body-wall of the collar, and that the remainder of its circumference is freely exposed to the collar-coelom. It is difficult to see the purpose of this arrangement; but I am inclined to think that the tissue must be interpreted as muscular; that the principal mode of contraction of the lamellae is along the line between the body-wall and the dorsal wall of the collar-canal; and that the effect of the contraction is to dilate the lumen of the canal and its aperture into the body-cavity.

It is now necessary to return to figs. 47—49, in which fibres can be traced from the dorsal wall of the collar-canal to the oral epidermis of the operculum. These figures refer to *C. gracilis*, and although the arrangement at first sight seems to differ from that which has been examined in *C. dodecalophus* and *C. levinseni*, I think that the difference is more apparent than real. Thus in other specimens of *C. gracilis* I have obtained evidence that the problematical tissue is composed of lamellae connecting the wall of the collar-canal with the external body-wall, an arrangement which is not precluded by figs. 47—49. Moreover, in the other species, there is evidence that certain fibres pass from the wall of the collar-canal to the oral wall of the operculum. This is shewn, in *C. dodecalophus*, in fig. 151, where in addition to the main mass of the problematical tissue (*x.*) a few delicate fibres, similar to the shorter fibres which traverse the collar-cavities in such numbers, pass from the wall of the collar-canal or even from the problematical tissue, to the oral wall of the operculum. A similar arrangement is seen, in neuter individuals of *C. sibogae*, in figs. 77, 78; and it is thus probable that the dilatation of the collar-canal may be partly effected by the contraction of these fibres.

I feel that I am far from having understood the mechanism of the collar-canals in *Cephalodiscus*, but their structural arrangements seem to me to indicate clearly that muscular action is an important factor in their mode of acting. The thin dorsal epithelium of the canals, and its varying position, suggest that the movements of this part are of importance, and it is not improbable that it may to some extent have a simple valvular action, controlled by the fluid pressure of the contents of the collar-cavity.

I have not noticed any differences of importance between the different species of *Cephalodiscus*

with regard to the structure of their collar-canals. The main relations of these organs seem to be quite invariable. The problematical tissue is more highly developed in *C. levinseni* than in *C. dodecalophus*. It is strongly developed in the neuter individuals of *C. sibogae*, in correlation with the muscular nature of the animal generally; and it is less conspicuous in *C. gracilis*.

IX. METASOME [1], BODY OR TRUNK.

This region, which is characterized by including the third body-cavities, differs in proportions in the different species, though there can be little doubt that the examination of contracted preserved specimens does not give a complete idea of its shape when the strong antero-ventral muscles are relaxed. The body is relatively short in *C. dodecalophus*, while the opposite extreme is reached in old individuals of *C. levinseni*, in which the form is elongated and cylindrical. *C. gracilis* and *C. sibogae* are intermediate between the other two species, in this respect.

The metasome contains the whole of the alimentary canal, with the exception of the anterior part of the pharynx, and it also includes the reproductive organs. Its junction with the collar is not well marked externally on its anterior side, although it is sharply marked internally by the septum between the second and third body-cavities, while the gill-slits open along the line of junction.

The alimentary canal and reproductive organs will be described below, and the present Section deals principally with the third body-cavity. The main part of this cavity is a well marked space, which is not obscured by connective tissue or muscles passing across it, as is the case in the other coelomic spaces. It is subdivided by a median dorsal and ventral mesentery, both of which are typically complete except for the fact that the ventral mesentery breaks down in the middle of the stalk. This region is, however, traversed, on its anterior and posterior sides by ridges (Pl. XI, figs. 132, 133) which indicate remains of the mesentery. The cavity of the stalk is usually filled by connective tissue, which ends sharply at the point where the stalk joins the body (Pl. IV, fig. 42). As the part of the ventral mesentery inside the body is attached along its whole length to the surface of this mass of connective tissue, there is no open communication between the two halves of the third body-cavity. The cavity is lined by a peritoneum, which invests the surface of the ovaries and the whole of the alimentary canal, but it does not pass into the region where the anterior wall of the intestine is in contact with the posterior surface of the stomach. Included in the principal bend of the alimentary canal, in the region of the second stomach there is, however, a small part of the body-cavity, which opens widely, on either side, into the main body-cavity. This can always be seen in sagittal sections, and it is marked *b.c.*[3]*b.* in Pl. IV, figs. 33, 34, 37, 38, 42. It is indicated by M'INTOSH (**87**) in his fig. 3 on Pl. III, and is alluded to as a "peculiar fold" in the wall of the alimentary canal (*t. cit.*, pp. 17, 41 note). The individual drawn in fig. 42 shews the arrangement described

1) The stalk is of course to be regarded as part of the metasome, but it may conveniently be considered in a separate Section.

by M'Intosh quite clearly in some of the more lateral sections. The suggestion naturally occurs that this arrangement may have some bearing on the manner in which the alimentary canal is differentiated in the bud; a question which is considered in Section XVI.

The opening of this part of the cavity into the general metasomatic cavities is shewn in Pl. XI, fig. 130 and in Pl. V, fig. 53. It is possible that the space is of functional importance in allowing the second stomach to alter its diameter more freely than would be the case if its movements were restricted by a close union of its wall with that of the principal stomach. As this region of the metasome is, moreover, probably exposed to considerable alterations in shape or position, by the contraction of the antero-ventral musculature, it is possible that the part of the body-cavity in question may have some importance in permitting a certain amount of sliding motion of the two limbs of the alimentary canal over one another, at the bend, thus allowing the second stomach to adapt itself to alterations in the position or direction of the stalk.

The peritoneal investment (*pt.*), which is further considered below, is often so loosely applied to the alimentary canal that a considerable space occurs between it and the digestive epithelium (figs. 43, 51—53). This is clearly to some extent the result of defective preservation, but I believe that the investment is in reality a somewhat loose one, in certain places at least, and that a splanchnic blood-sinus normally occurs below the peritoneum.

The ventral part of the anterior wall of the third body-cavities is specially concerned with the principal muscles, those which extend between septum $^2/_3$ and the tip of the stalk. A ventral horn (*b. c.*^{3} *a.*) extends, in the females, and in the neuter individuals of *C. sibogae*, along the anterior border of the gill-slits (figs. 68, 77, 123, 156) as far as the region of the collar-canals. These parts of the third body-cavity have already been discussed in the preceding Section, and are further described in Section XII, dealing with the musculature.

Mesenteries.

The mesenteries require separate treatment for the different species. In *C. dodecalophus* and *C. levinseni* the dorsal and ventral mesenteries are both complete, except in the axial region of the stalk, where the ventral mesentery breaks down in all the species.

In *C. dodecalophus* (Pl. XII, figs. 152—157) the dorsal mesentery (*mes.*^{3}) extends between the dorsal body-wall, the pharynx, the rectum and the dorsal caecum of the stomach; another detached portion of it bisecting the small cavity (Pl. IV, fig. 42, *b. c.*^{3} *b.*) seen in sagittal sections at the bend of the alimentary canal. The dorsal mesentery includes the well developed dorsal vessel. From the dorsal mesentery are given off the lateral mesenteries, which carry blood-vessels to the ovaries (Pl. XII, figs. 152—157, *ov. v.*).

The lateral or ovarian mesenteries (*ov. m.*) extend from the dorsal body-wall and the dorsal mesentery to the oviducts, terminating with a free edge ventrally slightly below the point where the oviduct joins the ovary (Pl. XII, figs. 149—156). It is thus only the extreme dorsal end of the ovary which is supported by the lateral mesentery. In the region where the oviduct opens to the exterior the lateral mesentery joins the dorsal body-wall (figs. 150—152).

The ventral mesentery (*v. mes.*^{3}) follows the convex side of the loop of the alimentary canal. The rectum and intestine are so closely pressed against the posterior body-wall that the

mesentery cannot always be detected in this region (figs. 152—157). In some cases, however, the posterior limb of the alimentary canal is seen to be suspended by an extremely short mesentery, the coelom thus intervening between the canal and the body-wall. In favourable specimens (fig. 157) the anterior part of the ventral mesentery is seen to include a small blood-vessel (*a. v'.*), which occurs at the junction of the mesentery with the body-wall. This vessel is the direct continuation of the anterior vessel (fig. 133, *a. v.*) of the stalk.

The mesenteries of the third body-cavity of *C. levinseni* agree in all respects with those of *C. dodecalophus*, as may be seen from the frontal sections shewn in figs. 120—130. The dorsal and lateral mesenteries are shewn in figs. 119—123. In figs. 124, 125, the lateral mesenteries have come to an end, while the dorsal mesentery continues uninterruptedly until the stomach is reached. Fig. 130 shews the detached part of the dorsal mesentery which occurs at the bend of the alimentary canal. The extreme anterior end of the ventral mesentery, with its blood-vessel, is seen in fig. 124, between the pharynx and the ventral part of the collar. The ventral mesentery can be seen, on the anterior and posterior sides of the alimentary canal, in the remaining sections figured (figs. 125—130).

In *C. gracilis*, perhaps in correlation with its smaller size, the mesenteries are less complete than in the two species so far considered. The dorsal mesentery is complete only at its extreme dorsal end (Pl. VI, fig. 67), while in sections nearer the stalk (figs. 68—70) it is represented merely by the dorsal vessel. The lateral mesenteries are similarly represented by the vessels to the ovaries (fig. 68). The ventral mesentery can be distinguished on the pharyngeal side (fig. 69) for a short distance beyond the collar-region, but it soon disappears completely (fig. 70), except so far as it is represented by the blood-vessel, which in favourable specimens can be seen on the inner side of the body-wall. The rectum is usually in such close contact with the posterior body-wall that no definite mesentery is formed on this side. A portion of the ventral mesentery persists near the base of the stalk, where it carries the posterior stalk-vessel to the bend of the alimentary canal (fig. 71). I have not detected any portion of the dorsal mesentery on the concave side of the bend, in the part of the body-cavity marked *b. c.*^{3} *b.* in fig. 37; but I am not prepared to say that it does not exist in that region.

It may be noted that the ventral mesentery is incomplete even in the buds of *C. gracilis* (Pl. V, fig. 56) whereas in *C. dodecalophus* the observations of Masterman (**98**, 2, figs. 52—58, etc.) shew that it is complete at a corresponding stage.

In the neuter individuals of *C. sibogae* the dorsal mesentery is incomplete (Pl. VIII, figs. 90, 91). The lateral mesenteries are not present, in consequence of the absence of gonads. The ventral mesentery is distinguishable, on the pharyngeal side, in the region of the gill-slits (fig. 92). In the males of the same species there are remains of the dorsal and lateral mesenteries (figs. 86, 87) and of the ventral mesentery (fig. 89).

The body-wall of the metasome is in most parts thin and without any specially noteworthy characters. The muscular layer is almost confined to the anterior surface (see Section XII). The epidermis may be pigmented, especially in *C. sibogae*, which is characterized by the presence, in practically all parts of the adult animal, of an unusually large amount of very dark pigment.

The dorsal epidermis in all the species consists, near the middle line, of a specially high columnar epithelium (*y*.) which is very conspicuous in *C. gracilis* (Pl. V, figs. 45—52) and in the neuter individuals of *C. sibogae* (Pl. IV, fig. 39). In the latter case, the organ is obviously ciliated, and appears to have a nerve-layer at its base. It is perhaps to be regarded as a sense-organ.

X. STALK

The stalk of *Cephalodiscus* is the muscular aboral part of the metasome. It consists of an epidermis, separated by a well marked basement-membrane from a strong mass of longitudinal muscles. The space surrounded by these muscles may be regarded as morphologically part of the third body-cavities, but it is usually filled by connective tissue to such an extent as to leave no definite cavity. The ventral mesentery is, in most cases, indicated by parts which enclose the two longitudinal vessels, but the mesentery does not appear to persist as a complete septum in the adults of any of the species. It has been pointed out by M'Intosh (**87**, pp. 20, 23) that the truncated base of the stalk is probably used as a sucker. It would be difficult to understand the mode of action of the powerful muscles of the stalk if the animal were not able to attach the base of that organ to the wall of its coenoecium.

The origin of the stalk from the body differs in the different species. In the buds it is invariably a direct prolongation of the rest of the metasome, as shewn for *C. dodecalophus* by Masterman (**98**, 2, Pls. II, III) or in my own figures of the same species (Pl. XIII, fig. 181) or of *C. gracilis* (Pl. I, fig. 4; Pl. III, fig. 32). In the adults of *C. sibogae* (Pl. I, fig. 3) this relation is but slightly modified, although even here the stalk originates somewhat on the anterior or pharyngeal side of the body. In the other species, the origin of the stalk is usually shifted towards the mouth, so that the ventral end of the body projects beyond it, on its posterior side, as a caecum containing the loop of the alimentary canal. But in one specimen of *C. gracilis*, I have observed a connexion of the stalk with the body precisely like that shewn, for *C. sibogae*, in fig. 3. The consideration of this case suggests that the appearance of the posterior caecum of the body is caused, to some extent at least, by the contraction of the longitudinal muscles which run from the stalk principally along the anterior side of the body, and that in the relaxed condition of these muscles the stalk would appear as an almost direct continuation of the body itself.

In *C. dodecalophus* the stalk is usually found directed towards the mouth, as in the well known figure given by M'Intosh (**87**, Pl. II), although the first figure on the next plate of the same author shews that it can be directed away from the mouth. In young individuals of *C. levinseni* (Pl. I, fig. 5) the stalk is usually in the position which is most commonly found in *C. dodecalophus*, lying beneath the edge of the proboscis, as in the specimen figured, or externally to that structure. In old individuals of the same species, I have invariably found it directed away from the mouth (fig. 6), usually describing a short spiral round the bud or embryos found in the proximal part of the zooecium. In *C. gracilis* and *C. sibogae*, I have

always found the stalk directed away from the mouth, except in cases where the metasome or the stalk itself is bent towards the mouth (cf. Pl. IV, fig. 40).

The structure of the stalk of *C dodecalophus* has been described by M'Intosh (**87**, p. 20, Pl. IV, fig. 5, etc.) and by Masterman (**98**, 2, p. 513, Pl. I, fig. 18). Masterman adds to the general description given by M'Intosh the account of three definite nerve-tracts on the "ventral" side of the stalk, and of a "dorsal" and "ventral" blood-vessel running along the remains of the mesentery found on opposite sides of the stalk. Each of the nerve-tracts is said to have a fine lumen.

I can confirm the accuracy of Masterman's account, except that I have not found a lumen in any of the nerve-tracts, and that I prefer to use the terms "anterior" and "posterior" instead of "ventral" and "dorsal" respectively.

The stalks in the "Challenger" material are very strongly contracted, as is indicated by the folding of the epidermis and of its basement-membrane as seen in longitudinal sections (Pl. XIII, fig. 169). These folds are responsible for the irregularities in the outline of the transverse sections. Pl. XI, fig. 133 shews the three nerve-tracts (*n. t.*) described by Masterman. These appear to be continuous with a general nerve-plexus lying at the base of the entire ectoderm of the stalk. The basement-membrane, internal to the nerve-layer, is deeply stained with haematoxylin, although its thickness appears greater than it really is in consequence of the extensive folding which has been alluded to. The membrane is prolonged inwards in the two median lines to support the anterior limb (*a. v.*) and the posterior limb (*p. v.*) of the loop of the ventral vessel which descends into the stalk. These prolongations of the membrane represent remains of the ventral mesentery, which is complete in the young buds (cf. Masterman, **98**, 2, p. 515), but cannot be recognized as a complete partition in the adult stalk. The remainder of the body-wall is constituted by a powerful development of longitudinal muscles, and the interval left free from muscles is entirely filled by an extensive development of connective tissue. The body-cavity of the stalk is thus virtual in the adult zooid.

The stalk of *C. levinseni* (Pl. XI, fig. 132) differs in certain respects from that of *C. dodecalophus*. It is more regular in outline, and its nerve-layer forms a single projection, triangular in transverse section, towards the interior of the stalk. The layer of longitudinal muscles is arranged very definitely, as a pair of oval groups of fibres, open towards the middle line. The connective tissue filling the cavity of the stalk is not so much developed as in *C. dodecalophus*. The two parts of the vascular loop are present as in that species, but the basement-membrane is not so thick.

The mode of origin [1]) of the stalk from the body is explained by figs. 125—128. In the sections nearer the mouth (Pl. X, fig. 125), the muscular layer is relatively thin, and surrounds the anterior third of the section, being divided into two halves by the ventral mesentery. In Pl. XI, fig. 126, the ventral mesentery has become incomplete, ending in a connective tissue layer which separates the internal tissue of the stalk from the general body-cavity. A small triangular space, doubtless part of the body-cavity, intervenes between the part of the mesentery

1) The other species agree, in essential respects, with *C. levinseni*, so far as the mode of origin of the stalk is concerned.

which is attached to the oesophagus and the part which bears the anterior limb of the vascular loop of the stalk. In fig. 127 the epidermis is raised up into a projection, inside which the musculature of the body-wall is taking on the arrangement characteristic of the stalk. The ventral mesentery passes from the stomach to the limiting layer of the connective tissue of the stalk, with which it is specially connected on the left side of the figure. The triangular space of fig. 126 is no longer distinguishable from the other spaces in the feebly developed connective tissue of the stalk. The muscles, in this and in other sections, have a tendency to arrange themselves in conuli, the apices of which project towards the centre of the stalk.

Fig. 128 cuts the stalk immediately before it separates completely from the body; and it thus shews the posterior limb (*p.v.*) of the stalk-vessel at the point where it enters the body. The anterior limb (*a.v.*) of the same vessel is still indicated by a thickening of this part of the mesentery. Fig. 132, which has already been described, is a section, somewhat more highly magnified, of the stalk of the same individual, through a part which has become completely separated from the body-wall.

It may be noted here that the stalk of *Rhabdopleura* has a structure essentially corresponding with that of *Cephalodiscus*. This follows from the recent accounts given by SCHEPOTIEFF (**04**, p. 10) and FOWLER (**04**, p. 24). The stalk of *Rhabdopleura*, is, however divided by a complete median mesentery. According to FOWLER's description and figure (Pl. III, fig. 2) a nerve-tract, triangular in transverse section, is found on the "ventral" side of the stalk, exactly as in *C. levinseni*. In the immediate neigbourhood of this is a space (*b*), regarded by FOWLER as perhaps artificial; while next to this, and almost in the middle of the mesentery, is another space marked by FOWLER *end.*? This cavity is "continuous with the lining of the alimentary canal" (p. 29), and FOWLER rejects the view that it is a blood-vessel, suggesting that it is an endodermic structure, which is concerned in the formation of the alimentary canal of the buds. This view is further alluded to in Section XVI, but in the mean time I may point out that the two cavities described by FOWLER in the stalk-mesentery of *Rhabdopleura* have precisely the same arrangement as the two parts of the vascular loop which extends into the stalk of *Cephalodiscus*.

The stalk of *C. gracilis* (fig. 134), differs from that of either of the species which have already been described. The epidermis of the anterior side forms a large ridge projecting towards the centre. This is usually bisected by a vertical line of pigment, on either side of which is a layer of nerve-fibrils. The ridge is relatively more prominent than in *C. levinseni*, and may be parallel-sided in transverse section. The muscular layer is reflected round this ridge; and while it thus has fundamentally the same arrangement as in *C. levinseni*, the shape of the muscular mass is somewhat different. Connective tissue is hardly developed in the stalk, which thus contains a definite cavity. The vessels of the stalk, instead of appearing as minute slits in the remnants of the mesentery, are commonly very conspicuous in transverse section, and appear as large cavities with a delicate wall. In some cases (fig. 134) they are obviously anterior and posterior in position, but they often lie side by side in the body-cavity of the stalk (fig. 135), although it can be ascertained, in some of these cases, that one of the vessels is closely related to the nerve-ridge of the anterior side of the stalk, while the other is suspended by an

inconspicuous mesentery from the posterior wall. It has been possible in this species, as in *C. dodecalophus*, to trace the vascular loop from the bend of the alimentary canal (Pl. III, fig. 22) down the posterior side of the stalk, while the anterior vessel of the stalk is continuous with the vessel in the ventral mesentery of the body. The stalk-vessels in this species have been observed to contain a distinct coagulum, confirming the view that they are really parts of the vascular system.

The stalk of *C. sibogae* (fig. 136) resembles that of *C. gracilis*. The muscular layer is composed of specially strong fibres, and the amount of connective tissue is small. The nerve-tract of the anterior side forms a prominent ridge. Remains of the mesentery can sometimes he distinguished on the anterior and posterior walls of the stalk, but the state of preservation is often too unsatisfactory to allow of the certain identification of the stalk-vessels.

A considerable number of stalks of *C. sibogae* end proximally in a single basal disc, one of which is shewn in vertical section in Pl. VIII, fig. 94. The individuals thus connected have presumably arisen by budding from a single parent zooid. A similar arrangement is found in *C. gracilis* and is described below, in connexion with the buds (Section XVI).

XI. ALIMENTARY CANAL.

The alimentary canal of all the species of *Cephalodiscus* is constructed on essentially similar lines. Its general features may most easily be studied in sagittal sections (Pl. IV).

If the orientation which is adopted in this Report be correct, the whole of the outer outline of the *U*-shaped tube may be described as ventral, and the whole of the inner outline as dorsal.

The size of the lumen of the several parts of the canal differs greatly in different individuals, the differences being due partly to age, and partly to the condition of muscular contraction of the body. One of the parts which shews the greatest variety of form is the mouth, the appearance of which is closely correlated with the attitude assumed by the proboscis.

In *C. dodecalophus* (fig. 42) the mouth (*m.*) is indicated by a rather sudden thickening of the epithelium on both its dorsal and ventral sides, giving rise to distinct upper and lower lips. The upper lip (*u. l.*) is continuous with the thin ventral epidermis of the proboscis-stalk, and it is in close relation with the posterior ventral horn of the anterior body-cavity. The lower lip passes into the inner epidermic layer of the operculum, a recess (*op. rec.*) being left between that organ and the lip when the operculum occupies the position shewn in fig. 42. This recess may be a conspicuous feature of sections through the oral region of some the species.

Immediately behind the upper lip is a conspicuous dorsal diverticulum (*div.*) of the pharynx (*ph.*). This diverticulum comes into close contact with the posterior end of the central nervous system (*c. n. s.*), and it forms a part of the division between the second and third body-cavities. From its anterior side originates the notochord (*nch.*), a tubular organ which probably

in all cases opens into the pharyngeal diverticulum, although the actual connexion can only be demonstrated in a certain proportion of cases (fig. 42; Pl. XIII, fig. 181). The pharynx (*ph.*) is a large organ, the walls of which are usually a good deal folded, a condition probably due not only to the contraction of its own longitudinal muscles but also to that of the anterior longitudinal muscles of the body. The pharynx passes into the oesophagus (*oes.*), which is well marked off from the pharynx, and opens into the middle of the anterior side of the large stomach (*stom.*), the walls of which are much folded. Near the junction of the stalk with the body, the stomach opens into a portion which may be called the second stomach (*stom.*^{2}), since the histology of its walls indicates that it has an important digestive function. The second stomach bends round the ventral wall of the stomach, from which it is separated by a part of the third body-cavity (*b.c.*^{3} *b*). On the termination of this part of the coelom it passes into the intestine, which is closely apposed to the posterior wall of the stomach. The junction between the second stomach and the intestine may be conspicuously indicated by a fold in the wall, as shewn by M'Intosh (**87**) in his Pl. III, fig. 3. This fold is well marked in some of the more lateral sections of the series from which fig. 42 is taken, but it does not appear in the section figured. M'Intosh remarks (p. 17) that "this peculiar fold..... probably indicates a tendency to "the formation of a second or pyloric stomach, as in *Phoronis*, and is therefore of considerable "morphological significance".

The dilated rectum (*r.*) is also partly attached to the stomach, on leaving which its dorsal surface is exposed to the third body-cavity. It opens to the exterior by the transversely elongated anus, which is not shewn in the figure. The walls of the intestine and rectum are thin and probably do not secrete digestive fluids. The size of the lumen of the rectum varies greatly in different individuals.

In *C. levinseni* (figs. 33, 34) the alimentary canal as a whole shares in the elongation of the body as compared with *C. dodecalophus*; but the same parts may be recognized. The dorsal diverticulum of the pharynx comes into less extensive contact with the central nervous system. In old individuals (fig. 33) the stomach may be greatly elongated, while the intestine (*int.*) may pass continuously into the rectum (*r.*) without shewing the dilatation which usually marks the beginning of the latter. This dilatation may, however, be as well marked in *C. levinseni* as in the other species, as is apparent from fig. 34 and from Pl. I, fig. 6. It may be enquired whether the difference between fig. 33 and fig. 34 is one of age or whether, on the contrary, it is not merely a difference in the state of muscular contraction. I regard the latter as the more probable explanation, particularly when the much greater antero-posterior diameter of fig. 34 is taken into account. If this be the case, the elongation of the body would appear to have the result of straightening out the rectum, the lobe which overlaps the stomach in fig. 34 being in fact the result of the contracted condition of the zooid. The elongation of fig. 33, as compared with fig. 34, has affected all parts of the alimentary canal to a greater or less extent. The oesophagus (*oes.*) is much drawn out, and the antero-ventral caecum of the stomach seen in fig. 34 has been obliterated in fig. 33. I have observed two or three neuter individuals of *C. sibogae* shewing the same excessive elongation that is noticeable in fig. 33; and it appears natural to regard these as the extended condition of the animal. It is probable

that the extension is effected by the attachment of the suctorial base of the stalk to the wall of the coenoecium, the animal then crawling on its buccal disc away from its fixed end.

The second stomach of *C. levinseni* (figs. 33, 34, *stom.*[2]) is more *U*-shaped than in *C. dodecalophus*. But a comparison of these figures with fig. 42 *(C. dodecalophus)* will shew that there is no essential difference, in this respect, between the two species; and it is not impossible that a less contracted specimen of *C. dodecalophus* might have its second stomach more in the position which appears to be characteristic of *C. levinseni*. In the latter the second stomach forms a considerable portion of the bend of the *U*-shaped tube, being about equally developed on both sides of the actual bend. Examination of entire specimens (fig. 6) shews that the folds of the second stomach are arranged in a spiral line, and it might indeed be said that they constitute a spiral valve. The two limbs of the alimentary canal are, as usual, separated from one another by a part of the third body-cavity (*b.c.*[3] *b.*), subdivided by a median partition (Pl. XI, fig. 130, *mes.*[3]) which must be regarded as part of the dorsal mesentery. The cavity of the rectum is usually large, and commonly contains a large mass of faeces, in which the remains of Diatoms may be distinguished. In several of the specimens (as in the one shewn in fig. 34) a quantity of these faeces is passing out of the anus, which accordingly appears widely open.

The alimentary canal of *C. gracilis* is shewn in fig. 37. The second stomach leaves the stomach at the end of its main axis, as in *C. levinseni*, and forms a wide cavity which extends on both sides of the bend of the alimentary canal. The third body-cavity passes, as usual, between the two limbs of the second stomach, but the space shewn in fig. 37 between the stomach and the intestine is not lined by peritoneum and is probably an artefact.

My examination of the alimentary canal of *C. sibogae* (neuter forms) has been complicated by the unsatisfactory state of preservation of the material. Sections of the mass of zooids still contained in the basal coenoecium were not satisfactory; and it was very difficult to isolate zooids in an uninjured condition. My results indicate, however, a great elongation of the alimentary canal in the adult and uncontracted zooids. In fully extended specimens (fig. 38) the second stomach appears to pass off from the extreme ventral end of the elongated stomach, and the form of the entire canal is thus more simply *U*-shaped than in any of the other species. Fig. 40, taken from an entire specimen, shews a condition which is probably due to contraction of the body, the bend of the canal being reflected towards the anterior side of the stomach In the uncontracted condition of this specimen it is probable that the position of the second stomach would have been as in fig. 38.

The structure of the mouth and pharynx of *Cephalodiscus* require a somewhat detailed description, which may be preceded by one or two remarks on that of the remaining parts of the alimentary canal, and on the nature of the food.

The structure of the oesophagus resembles that of the pharynx, of which it is indeed merely a division. But it is always to be recognised, in suitable preparations, and hence deserves a special name. It is probably a sort of ante-chamber to the stomach, through which food passes by definite swallowing actions when a sufficient quantity has accumulated in the pharynx.

Its walls are usually thinner at each of its lateral edges than elsewhere (Pl. XI, fig. 126), indicating the power of dilating and contracting in a definite way. Its posterior aperture commonly projects into the stomach in the manner shewn in figs. 34, 42 (Pl. IV).

The stomach has high, glandular walls which are almost certainly pigmented. The epithelium is usually not well preserved. The shape of the cavity is complicated by numerous folds, which in entire zooids, both of *C. dodecalophus* and of *C. levinseni*, are seen to be arranged principally in the frontal direction. This may indicate that they are partly due to the general contraction of the body-musculature.

The second stomach, which opens from the main organ, has an epithelium which appears to be glandular, and is considerably higher than that of the succeeding part of the canal. It may be presumed that digestion is continued in this part.

The intestine may be considered to begin at the point where the coelom which extends between the two limbs of the *U*-shaped loop of the alimentary canal ends (figs. 34, 37). Its relatively thin walls pass continuously into the higher epithelium of the second stomach on the one hand and into those of the rectum on the other hand. The rectum is merely a part of the intestine, with which it is perfectly continuous, but the name may conveniently be employed for the last part of the alimentary canal, the dorsal wall of which is exposed to the third body-cavity. The size and shape of the rectum differ according to the state of contraction and the development of other organs. Thus in fig. 42 the small lumen seen in the rectum appears to be due to the specially large size of the ovary.

The food of *Cephalodiscus* seems to consist principally of microscopic organisms. The cell-walls of Diatoms are found in various parts of the alimentary canal, with other detritus, among which Sponge-spicules can often be recognised. But in addition to the smaller particles, larger organisms are occasionally found. Thus a considerable part of the intestine and rectum of the individual of *C. levinseni* shewn in fig. 33 is occupied by an organism which seems to be a Copepod in a partially digested condition. I have found a similar case in a specimen of *C. dodecalophus*, while the individual of this species shewn in figs. 152—155 has in its stomach what appears to be a Polychaet, some of the long cirri of which are imbedded in the digestive epithelium. I am inclined to regard this as a case of parasitism.

Mouth, Pharynx and Notochord.

The study of the commencement of the alimentary canal is of special importance in connexion with various physiological problems, and specially in the consideration of the probable mode of feeding. As in the case of several other parts of the animal, it is by no means easy to distinguish between temporary folds due to contraction and grooves or ridges which are permanent, and of morphological or physiological importance; while the varying positions assumed by the proboscis-stalk, the arms and the operculum introduce further difficulties in interpreting the structure of the mouth.

In the account which MASTERMAN (**98**, 2, p. 507) has given of the mouth and pharynx, the food-grooves of the arms are said to be continuous with certain grooves on the inner side of the wall of the pharynx. The grooves unite, two by two, so as to form a system of three lateral "oral grooves" which enter the mouth on each side (figs. 1, 2)[1]. These proceed posteriorly and dorsally and finally form a large median dorsal hyperpharyngeal groove (figs. 4—9). The gill-slits are indicated as two ventro-lateral-channels even in sections immediately behind the mouth (figs. 2, 3), while further back their walls are seen to be continuous dorsally with the "pleurochords", and to be formed of the same sort of tissue (fig. 8). The alimentary portion of the pharynx commences as a median ventral groove (fig. 4) between the two gill-pouches, and soon forms a large section of the pharynx lying ventrally to these structures (figs. 5—9). Figs. 90—92 shew that the dorsal diverticulum of the pharynx has 4 grooves, two dorsal and two ventral (or, as I prefer to call them, posterior and anterior, respectively), the section of the lumen being hence quadrangular. The four grooves are directly continuous with the lumen of the notochord (MASTERMAN's "subneural gland"). The two "dorsal" grooves pass down the dorsal wall of the pharynx and are traceable as far as the commencement of the oesophagus, being situated on the median side of the pleurochordal outgrowths, in the region of those organs (figs. 93—99). The "ventral" grooves of the pharyngeal diverticulum pass down the sides of the mouth (fig. 93, *v.g.*), ventrally to which they unite, in course of time, to form the large median alimentary part of the pharynx. This again can be traced to the beginning of the oesophagus; and the lumen of the posterior end of the pharynx is thus triradiate in section (two dorsal grooves and one ventral groove). By the median union of the two "ventral" grooves of the pharyngeal diverticulum a "peri-pharyngeal band" is constituted. This, if I understand MASTERMAN correctly, is joined by the oral grooves on the anterior side of the pharyngeal diverticulum.

MASTERMAN recognises that the grooves which he has described are too small to allow the supposition that the water-currents carrying the food pass along them, and he has suggested that they direct the flow of a secretion of mucus by which the food-particles are entangled and are thus prevented from being washed out through the gill-slits. Here I think he is right, although he guards himself from expressing any very definite opinion as to the direction of the flow of mucus. The notochord is, however, regarded as a mucus-secreting organ, while the pleurochords serve partly as a channel through which any excess of water which has passed to the posterior end of the pharynx travels forwards in order to issue at the gill-slits. This view is illustrated by MASTERMAN's diagrammatic fig. 100.

It is obvious from a consideration of the sagittal sections figured in Plate IV that the relations of the mouth depend greatly on the position which the anterior end of the animal, and in particular the proboscis, happens to occupy. Thus in *C. levinseni*, the pharyngeal diverticulum in fig. 33 has its opening directed towards the anterior side of the animal, while in fig. 34 it is directed ventrally. In the one case, a series of sections transverse to the long axis of the

1) These references relate to the figures given in Plates I and V of MASTERMAN's paper. Figs. 1—9 are from a transverse series of the whole animal, passing therefore transversely through the beginning of the alimentary canal, and longitudinally through the main part of the pharynx. Figs. 90—99 are transverse to the long axis of the animal, and are therefore what I term "frontal".

individual would have cut the upper lip before any part of the diverticulum was reached, and in the other, the first part to appear in the sections would have been the caecal end of the diverticulum (as in MASTERMAN's figs. 90—92). The arrangement of the oral or pharyngeal grooves seen in the sections would thus have been very different in the two cases. Figs. 37 and 43, of *C. gracilis*, illustrate the same point. On the other hand it is clear that in the case of an organ whose walls are so crumpled as is the pharynx in fig. 42, considerable care is necessary to distinguish the permanent folds from those which have no definite significance.

In describing my own observations I begin with the consideration of a frontal series of sections of a comparatively young blastozooid of *C. dodecalophus*, in which the structure appears to be but little complicated by secondary folding. The first section figured (Pl. XII, fig. 152) is dorsal to the mouth, and passes through the external aperture of the right oviduct, the dorsal diverticulum of the pharynx (*div.*) and the notochord (*nch.*). All the body-cavities are visible, the third cavity being subdivided on each side by the ovarian mesentery (*ov. m.*). On the left side, the section passes through the arm-base, just dorsally to the beginning of the operculum. On the right side, the lateral lobe of the operculum (*op. r.*) is cut in the main parallel to its flat surfaces; and the tentacles of the third and fourth arms are visible. The dorsal diverticulum of the pharynx is circular in section, its cavity being markedly triradiate. One of the grooves of the cavity is median and posterior, though shewing indications of being composed of MASTERMAN's two "dorsal grooves", the other two are paired and on the anterior side. Each of the three ridges which separate the grooves from one another is marked by a deeply stained patch of cells which appear to be glandular. In more dorsally situated sections the glandular area is continuous round the anterior side of the diverticulum; while more ventrally, patches which stain in the same way and seem to be unicellular glands, appear here and there on the lower lip, at the sides of the mouth, and even in the oral epidermis of the operculum.

In the next section but one (not figured) the base of the notochord is cut longitudinally (cf. Pl. IV, fig. 42), its lumen being traceable into the outer part of the anterior ridge of the pharyngeal diverticulum.

In fig. 153 (two sections later) the left lateral lobe of the operculum (*op. l.*) is cut horizontally, a fold (*f.*) of its body-wall marking off the section of the collar-cavity which contains the collar-canal from the more externally placed operculum itself. The section passes just ventrally to the base of the notochord, which is of course not seen. The pharyngeal diverticulum has much the same structure as in the former figure, except for the fact that the dorsal walls of a pair of lateral outgrowths of its cavity are involved by the section. The posterior ends of these walls are composed of a tissue which stains but slightly, and they constitute the beginning of what MASTERMAN (**97**, 2, p. 353, note) has described as the "pleurochords". I make use of this term for descriptive purposes without in any way accepting the homology indicated by MASTERMAN in using it.

Somewhat further ventrally (fig. 154) the lateral outgrowths open into the median part of the diverticulum, the pleurochordal tissue in their walls being sharply marked. The three grooves seen in the lumen of the median part are present as before.

Fig. 155 cuts the dorsal edge of the mouth; and the left anterior groove is seen to

open immediately behind an epithelial ridge (*e.r.*) which is visible in the former figures projecting from the anterior side of the arm-base into the space between the proboscis and the collar. The furrow on the median side of the ridge also opens into the mouth in the next section but one. A similar arrangement is indicated on the right side, except that the posterior groove is bifurcated at its internal end: the section being here at a slightly more dorsal level, the grooves do not appear to open into the mouth. The posterior median groove of the diverticulum is dying away, and the pleurochordal outgrowths are becoming larger.

Fig. 156 cuts the mouth (*m.*) and both the gill-slits (*g.s.*), the walls of the latter being mainly composed of pleurochordal tissue; while fig. 157 shews that the pleurochordal tissue is continued, in the walls of a pair of postero-lateral grooves of the pharynx, beyond the internal openings of the gill-slits. There can be no question that, in this specimen, the posterior groove of fig. 152 dies away between figs. 155 and 156, merging gradually into the surface of the convex epithelium of the posterior wall of the pharynx; and that it cannot be traced beyond the pleurochords, as indicated in MASTERMAN's figs. 93—99. The median part of the operculum in this individual is hanging ventrally from the mouth as an apron-like flap covering part of the anterior surface of the body.

Comparing these sections with the sagittal section, Pl. IV, fig. 42, it appears that the two grooves on each side of the middle line, opening into the mouth in fig. 155, pass horizontally on one of the ventro-lateral sides of the upper lip to the ventral end of the anterior wall of the pharyngeal diverticulum; and that they here meet the two vertical anterior grooves of that cavity. They are clearly the structures which MASTERMAN (**98**, 2, p. 507) describes as the "oral grooves". These are seen passing along the sides of the mouth in figs. 2—5 given by that author, while fig. 6 cuts the anterior wall of the pharyngeal diverticulum (as is shewn by the position of the notochord), the oral grooves opening into that structure on either side of the median ridge, which is also shewn in my own fig. 152. MASTERMAN's fig. 7 accordingly passes through the middle of the pharyngeal diverticulum.

The oral grooves are well seen in a plasticine reconstruction (fig. 24) which I made from a series of more or less transverse sections through an individual of *C. levinseni*; and in this case three oral grooves are distinctly indicated on each side.

Although I am thus able to confirm this part of MASTERMAN's results I do not find complete regularity in the arrangement of the oral grooves, which are not always symmetrical on either side of the middle line (fig. 155). A transverse section across the upper lip of *C. dodecalophus* shews a conspicuous median ridge projecting into the mouth. This is derived in front from the ventral wall of the proboscis, and further back from the collar, as will be obvious by reference to fig. 42. On either side of the median ridge, there may be only a single lateral ridge, so that two principal grooves pass along each side of the lip, as shewn in fig. 155. The bifurcation of the lateral ridge may give rise to three grooves on one side. In fig. 24 *(C. levinseni)* there may be two ridges on each side, in addition to the median ridge which projects from the proboscis-stalk; and three pairs of oral grooves are thus constituted.

Even when I have found three oral grooves, on each side, I have not succeeded in

shewing the continuity which MASTERMAN describes between each one of them and two of the arms. On the contrary, the arm-grooves, in many favourably orientated specimens, die away in approaching the mouth, and the inner surface of the arm-base becomes smoothly convex in places where grooves ought to occur on MASTERMAN's hypothesis. This is seen, for instance, in figs. 143—147 (Pl. XII), figs. 66, 65 (Pl. VI) and figs. 47—45 (Pl. V).

In order to obtain as much certainty as possible with regard to the relations of the oral grooves, I made plasticine reconstructions of two individuals of *C. gracilis*, namely those from which fig. 25 and figs. 62—70 were respectively drawn. I failed in these to find any evidence of continuity between the oral grooves and the food-grooves of the arms.

It may further be remarked that it is improbable, on *a priori* grounds, that a system of small grooves could be effective in all the parts where they have been described by MASTERMAN, who has himself (**98**, 2, p. 509) seen the difficulty of supposing that they could direct the flow of water.

I come next to the pair of "ventral grooves" described by MASTERMAN (**98**, 2), and marked *v.g.* in his fig. 93. These grooves, which are supposed to start as the "ventral" or anterior grooves of the pharyngeal diverticulum, pass down the sides of the mouth, just inside the oral aperture, and can then be recognised "by the fact that they are situated exactly internal "to the line of junction of the mesentery between collar- and trunk-cavities, with the gut wall". They are thus shewn in MASTERMAN's fig. 93, though not on the left side of fig. 16 of his earlier paper (**97**, 2), to which a reference is expressly given. In this latter figure, the left groove lies entirely in the region of the collar-cavity.

The series of sections from which figs. 152—157 are taken shews the "ventral" grooves in an unmistakeable form in the pharyngeal diverticulum (figs. 152, 153); but on passing to the mouth they communicate with the oral grooves (figs. 154, 155), and no trace can be seen of them in fig. 156, which passes through the mouth. I am satisfied that the grooves are really absent in this section, but the discrepancy between MASTERMAN's results and my own is not hard to explain. The parts of the "ventral grooves" which MASTERMAN shews at the sides of the mouth appear to me to be outside the mouth, and to belong to the recess (Pl. IV, figs. 34, 42, *op. rec.*), external to the oral aperture, which is formed by the base of the operculum. The recess may altogether disappear when the operculum is straightened out and its free edge is directed ventrally, as in figs. 156, 157, but it becomes conspicuous in certain other positions of the operculum.

Figs. 119—123 (Pl. X) are frontal sections of *C. levinseni* which shew what I think there can be no doubt are the parts of MASTERMAN's "ventral grooves" that are supposed to extend along the sides of the mouth. In fig. 123, the groove on the right side is continuous with a part of the basement-membrane extending, from the anterior horn of the third body-cavity (*b.c.*^{3}*a.*), between the collar-cavity (*b.c.*^{2}) and what may be an oral vascular sinus (*or. s.*). On the left side, the wall of the groove projects into the collar-cavity. These are so much like the relations shewn by MASTERMAN in fig. 16 of his earlier memoir (**97**, 2) that there can be no reasonable doubt that the grooves are the ones alluded to by him. But a further consideration of figs. 119—123 and of the other sections belonging to the same series shews that the two "ventral grooves" represent the junction of the base of the operculum with the mouth, and that

in this position of the operculum there is an epidermic recess (*op. rec.*) which opens into the pharynx by the mouth (*m.*). I am thus inclined to believe that the mouth in fig. 93 of MASTERMAN's later memoir (**98**, 2) is the aperture immediately internal to the "ventral grooves".

The epidermic recess which I describe is not in any way continuous with the ventral groove of the pharynx, but it comes to an end, as it began, on the outer side of the mouth, ceasing to be visible in the sections immediately after the mouth is passed. This indeed might be anticipated from the sagittal sections shewn in Plate IV.

The extra-oral "ventral grooves" are seen, in *C. gracilis*, in the sections shewn in figs. 66, 67 (Pl. VI). In the case of this individual I have made a plasticine reconstruction from the actual sections; and there can be no question, from the examination of this reconstruction, that the grooves are merely the junction of the operculum with the rest of the body, and that they have no relation to any grooves of the pharynx itself.

In fig. 3 of MASTERMAN's memoir a depression on each side of the ventral wall of the pharynx, immediately adjacent to the mouth, is identified as the beginning of a gill-slit. I do not understand how the gill-slit is supposed to occur in this position. An inspection of figs. 152—157 (Pl. XII) will shew that the first indication of the gill-slit appears in connexion with the dorsal side of the pharynx, as indeed MASTERMAN has himself pointed out, in insisting on the close connexion between pleurochords and gill-slits. In fig. 153 the dorsal ends of the pleurochords are seen as vacuolated tracts of the lateral pharyngeal epithelium, and distinctly on its dorsal or posterior side. The exact point at which these will open into the diverticulum is indicated in this section by a pair of minute depressions of the epithelium which are somewhat nearer the posterior than the anterior wall of the cavity. In fig. 154 the pleurochordal grooves are well established, while on the right side of fig. 155 the anterior end of the groove is recognisable as the dorsal wall of the gill-slit. In fig. 156 both gill-slits are completely formed, while in fig. 157 the vacuolated tissue of the pleurochords extends along the sides of the pharynx, beyond the points where the gill-slits have been given off. The tissue gradually fades away in passing along the sides of the pharynx, and it disappears completely some time before the oesophagus is reached.

With the exception of the point I have indicated with regard to the origin of the gill-slits, all this is completely in accordance with MASTERMAN's accounts of the pleurochords (**97**, 2, **98**, 2).

The close relation between the gill-slits and the dorso-lateral or pleurochordal grooves of the pharynx is shewn in the reconstruction of *C. levinseni* drawn in fig. 24 (Pl. III). The cavity of the pharynx is exposed by the removal of its anterior or ventral half, the whole of the upper lip and of the pharyngeal diverticulum being left. In the lower part of the figure is seen the posterior or dorsal wall of the pharynx, with a strongly convex surface, on either side of which are the two pleurochordal grooves. These become much deeper in passing forwards and they finally pass into the sides of the pharyngeal diverticulum, from which the tubes leading to the gill-pores open. In the dorsal view of the same specimen (fig. 23) the wall of the left gill-slit is seen curving outwards from the region of the diverticulum to open by its external aperture. The same relations are illustrated by figs. 121—123 (Pl. X). In fig. 123, the dorsal wall of the pharynx is convex towards the lumen of that organ, and on either side of it is one

of the dorso-lateral pleurochordal grooves, continuous on the one hand with the gill-slit, and on the other hand extending towards the pharyngeal diverticulum (figs. 122, 121). Fig. 129 (Pl. XI), of the same species, illustrates the same point. Figs. 45—47 (Pl. V), of *C. gracilis*, further shew that the gill-slits curve from the region of the pharyngeal diverticulum in an antero-ventral direction to their external apertures.

The gill-slits of the neuter individuals of *C. sibogae* are essentially similar to those of the other species, but they are associated with an unusually strong development of pleurochordal tissue in the more posterior („ventral") part of the pharynx.

The probable mode of action of the arrangements which have just been described may now be considered. I am quite inclined to accept MASTERMAN's view that an essential part of the feeding mechanism of *Cephalodiscus* is afforded by a secretion of mucus which entangles the organisms brought by the ciliary currents of the tentacles, and prevents them from being carried out through the gill-slits. It may be presumed that a current of considerable force passes through these apertures; and the need for some entangling mechanism seems probable. I am disposed to think that the mucus required by this hypothesis is secreted by the glandular patches shewn in figs. 152—154 (Pl. XII) in the walls of the dorsal pharyngeal diverticulum, and by unicellular glands in the walls of the mouth and on the base of the operculum. MASTERMAN ascribes the secretion to the notochord, which he terms the "subneural gland"; but it must be noted that whereas the structures which I regard as mucus-glands shew a strong affinity for haematoxylin, the notochord on the contrary takes up staining matter to a slight extent.

If this be the case, the anterior grooves seen in the pharyngeal diverticulum (figs. 152, 153) may be supposed to convey the mucus towards the mouth. Here it probably passes along the oral grooves to the great food-channels limited by the posterior wall of the proboscis and the anterior wall of the collar. There are not wanting indications that arrangements exist which might be capable of directing the mucus for a short distance along paths external to the mouth, perhaps during a temporary cessation of the ciliary current of the tentacles. Figs. 152—155 shew a perfectly definite epithelial ridge (*e.r.*) which is continuous with the ridge dividing the two principal oral grooves on each side, and can be traced for some distance along each side of the proboscis-stalk. It is probable that this ridge corresponds with the division of the arms of its side into two groups of three. Traced in a dorsal direction, the ridge becomes a groove at exactly the level where the arm-base meets the operculum. This transformation is effected by the appearance of another epithelial ridge on the median side of the first one, a process which has already been effected in fig. 152 on the right side, where *e.r.* is the ridge that is continuous with those seen in figs. 153—155. The higher ridge immediately in front of it passes some distance along the proboscis-stalk, dying away at the level of the proboscis-pores.

It appears to me probable that the effect of this arrangement is as follows. The mucus leaving the mouth by the outer oral grooves seen in fig. 155 probably passes along the oral surface of the operculum and soon comes into the region of the posteriorly directed food-grooves of arms 4—6. Immediately on the dorsal side of fig. 152 the ridge *e.r.* becomes continuous with the ventral side of the arm-base, which is traversed in an antero-posterior direction by the

groove marked *R.* 4—6 in fig. 152. This groove, which is of course open ventrally, may be no more than a temporary fold of the arm-base, but it indicates the path which the food-particles must take in passing from arms 4—6 along the ventral side of the arm-base to the food-passage which is bounded in front by the posterior wall of the proboscis. It thus appears that mucus passing along the anterior face of the operculum in figs. 155—152 would be brought into relation with the food-grooves of the posterior set of arms. The mucus leaving the mouth by the more median oral groove in fig. 155 would for the most part remain on the same side of the epithelial ridge *e. r.* (figs. 154—152), while the additional ridge seen between *e. r.* and the proboscis on the right side of fig. 152 would keep the mucus from passing further along the dorsal wall of the proboscis; and would, on the contrary, direct it to the region of the food-grooves of the first three arms.

The mucus which passes down the posterior wall of the pharyngeal diverticulum, whether in one or two grooves, might spread itself out on the dorsal wall of the pharynx, where it would be well placed to entangle food when the pharyngeal diverticulum had the position seen in figs. 33, 37 (Pl. IV).

Some at least of the food, entangled in the mucous secretion, is probably caught by the operculum and passes to the bottom of the opercular recess (*op. rec.*) indicated in figs. 34, 42. Here I imagine it to accumulate and from time to time to be taken into the pharynx by a definite swallowing action, due probably to the intrinsic muscles of the operculum (cf. Pl. IX, fig. 107). It then probably passes down the more median parts of the pharynx, along the deeply staining and almost certainly ciliated cells which constitute both its anterior and posterior wall. I think that Masterman is probably right in suggesting that the relation of the gill-slits to the pleurochordal grooves is to be explained by supposing that the excess of water which passes to the oesophageal end of the pharynx travels forwards along the grooves to issue by the gill-slits. The relation of the grooves to the pharyngeal diverticulum further suggests that this return current of water, entering the diverticulum from behind, would also have the effect of carrying the mucus forwards along the grooves of the upper lip to the point where it meets the inrush of water caused by the ciliary action of the tentacles. Finally it appears to me possible, from a consideration of such preparations as figs. 123—125 (Pl. X) that the lumen of the pharynx is not necessarily widely open during the whole process of feeding. It seems possible that the anterior and posterior walls of the pharynx may be apposed to one another in such a way as to close the cavity. This might happen during the accumulation of food in the opercular recess, the water meanwhile passing directly to the exterior by the gill-slits.

As actual evidence of the existence of mucus in connexion with the feeding process it may be remarked that M'Intosh (**87**, p. 16) in describing the structure of the pharynx states that in some preparations a film occurs on the surface of the epithelium which "is evidently due to mucus". I have observed appearances in sections of *C. dodecalophus* which point in the same direction, the film in question occurring not only along the free ends of the epithelial cells of the pharyngeal diverticulum, but also along those of the cells of the anterior and posterior walls of the pharynx, throughout the whole length of that organ, and even on those parts of the operculum and proboscis which are near the entrance to the alimentary canal.

The pharyngeal epithelium of *Cephalodiscus* closely resembles in structure the epidermis of the oral side of the operculum, with which it is continuous through the mouth. It is composed, for the most part, of deeply staining cells, with numerous nuclei in many layers. These probably indicate a columnar epithelium composed of very long and narrow cells. Clear evidence of ciliation is noticed in various preparations, and it is probable that the whole of the epithelium which has this character is ciliated. The remainder of the pharyngeal epithelium consists of the dorso-lateral regions which MASTERMAN has termed the "pleurochords", and of the walls of the gill-slits with which these are continuous. The epithelium is here vacuolated, and takes up staining materials with much less readiness than the other part, the nuclei being much less numerous.

The differentiation of the pleurochords is of course well marked in *C. dodecalophus*, and it is also particularly evident in the neuters of *C. sibogae*. In this case the distinction between the deeply staining epithelium of most of the pharynx and the slightly stained pleurochords is very marked. The species seems to be further remarkable for possessing an unusually distinct hypopharyngeal groove (Pl. VIII, figs. 90—92). It is difficult to speak with certainty as to the reality of a distinction, in this respect, between the species, as the condition of the pharynx differs so widely, in different individuals of the same species, in different degrees of contraction. Thus *C. dodecalophus* may have a very well marked median ventral groove, while in fig. 157, for instance, nothing of the kind is visible. In *C. levinseni* the pharynx is usually found flattened in an antero-posterior direction.

Notochord.

I use this term as indicating the homology of this organ with the structure in Balanoglossus called by that name by BATESON (**84**, p. 228; **86**, pp. 550, 562) and compared by him with the notochord of Chordata. Whether the latter homology holds good is an open question, but I think there can be no doubt that the "notochord" of *Cephalodiscus* is the homologue of the "notochord" of Balanoglossus. The organ has been termed the "Eicheldarm" by SPENGEL (in Balanoglossus), the "stomochord" by WILLEY (**99**, 1, p. 234; **99**, 2, p. 224) and the "subneural gland" by MASTERMAN (**97**, 2, p. 351).

The notochord of *Cephalodiscus* is a tubular [1]) structure which probably always opens into the anterior wall of the dorsal diverticulum of the pharynx (fig. 1 on p. 23), although the opening is not as a rule easy to demonstrate. The organ lies in septum $^1/_2$, on the dorsal side of that part of the anterior body-cavity which lies in the proboscis-stalk (Pl. IV, figs. 33, 34, 42; Pl. XIII, fig. 181; Pl. X, figs. 113—117) and on the ventral side of the two collar-cavities. The dorsal mesentery of the collar supports the notochord along its whole length; and, as is well shewn in MASTERMAN's figures (**03**, Pl. XXXII, figs. 1, 2), the length of the mesentery becomes less as it passes forwards, so that at its apex the notochord almost reaches the central nervous system. At its anterior end the notochord is intimately connected with the pericardium (Pl. IV, fig. 33; Pl. XIII, fig. 181; Pl. XI, fig. 138) to which its relations are the same as those found in Balanoglossus. The resemblance to this animal is further increased by the presence of a glomerulus (see p. 29) on the ventral side of the notochord.

1) SCHEPOTIEFF (04, p. 15) denies the tubular character.

MASTERMAN (**97**, 2, p. 351) states that the cells of the notochord of *C. dodecalophus* are ciliated internally, and that it may contain in its lumen a rod of mucus. In a later memoir (**03**, p. 718) he describes a vacuolated or "chordoid" appearance at the anterior end of the organ. I have observed a stained appearance in the lumen of the notochord in this species which may indicate the presence of mucus, but I feel extremely doubtful with regard to the existence of cilia, and I am not convinced that there is sufficient justification for speaking of a chordoid modification of the tip of the organ.

The large relative size of the notochord in the buds of *C. dodecalophus* (Pl. XIII, fig. 173) — a fact already noticed by M'INTOSH (**87**, p. 28) is of considerable interest as indicating the morphological importance of this structure. It is further noteworthy that the organ is specially large in the buds of *Rhabdopleura*, as appears from the observations of FOWLER (**04**, Pl. III, fig. 15). In the adult condition it retains its greatest relative size in *C. levinseni* (figs. 33, 23, 24, 113) where its tubular nature is specially obvious. In the more delicate *C. gracilis* (figs. 44, 64) and *C. sibogae* (Pl. VIII, fig. 93) the notochord is small; and in unfavourably orientated sections it is not always easy to demonstrate its existence. There is no doubt, however, of its presence in all the species which I have investigated, and it may be detected even in the males of *C. sibogae* (Pl. VIII, figs. 82, 83).

The homology of the notochord of *Cephalodiscus* with that of the Enteropneusta was at one time denied by MASTERMAN (**97**, 2, p. 351; **97**, 3), who has, however, more recently (**99**, 2, p. 362) admitted that it corresponds with the "vermiform process" of certain Enteropneusta. WILLEY (**99**, 1, p. 237) had shortly before maintained the same view.

It appears to me that it is unnecessary to suppose that the notochord of *Cephalodiscus* corresponds merely with the vermiform process. It is true that on a former occasion (**97**, p. 343) I pointed out, in answer to MASTERMAN's statement that the notochord of *Cephalodiscus* differs histologically from that of "every other notochord yet described", that it did not differ histologically from the anterior part of the notochord of *Schizocardium* and *Glandiceps* known, from SPENGEL's description, as the vermiform process. But I also called attention to the small size of *Cephalodiscus*, a fact which might be expected to be correlated with some simplification of the organs as compared with those of the Enteropneusta. The relation of the notochord of *Cephalodiscus* to the pericardium and to the proboscis-pores appears to me to lend no support to the view of WILLEY and MASTERMAN that the organ corresponds with the vermiform process alone. The process in question, as figured by SPENGEL (**93**, Pl. XII, fig. 2 and Pl. XX, fig. 1), lies entirely in front of the region of the pericardium and of the proboscis-pores, while the notochord of *Cephalodiscus* extends no further forward than this region. As moreover, the base of the notochord agrees, in its relation to the upper lip and to the ventral part of the anterior body-cavity, with the base of the "Eicheldarm" in the Enteropneusta, it seems to me reasonable to suppose that the notochord of *Cephalodiscus* corresponds with the entire "Eicheldarm", and not with the narrow anterior portion of it whose occurrence is limited to a small proportion of the species of Enteropneusta.

XII. MUSCULAR SYSTEM.

The strong development of the muscles in *Cephalodiscus* indicates a great amount of contractility. The system consists almost entirely of longitudinal fibres, which pass from the stalk to the proboscis, interrupted by the two transverse septa of the body-cavity. The more important muscles of the metasome pass along the anterior surface of the body-wall, in correlation with the origin of the stalk from this surface. The strongest muscles of the collar pass right and left of the mouth, while those of the proboscis diverge from septum $^1/_2$ and after traversing the anterior body-cavity are mainly inserted into its anterior wall. The muscular fibres probably originate and are inserted into some part of the basement-membrane which lines the body-cavity, important groups of the muscles ending in the transverse septa.

The muscles of the stalk have already been described (p. 51). Tracing these forwards, it will be found that at the junction of the stalk and body (Pl. XI, figs. 132, 128, 127, 126) the closed circle, or rather double crescent, of the stalk-muscles opens out on its posterior side, and the two ends of the series of muscles become reflected on to the anterior wall of the body. The muscle-fibres are still invested by an amount of connective tissue varying with the species, and the ventral mesentery of the metasome fades away in this mass of connective tissue. In passing into the body the muscular layer soon spreads along the adjacent parts of the body-wall (Pl. X, fig. 125; Pl. XII, fig. 157), thereby distributing the stress exerted by the contraction of the stalk-muscles. Most of the fibres pass in the direction of the mouth, along the anterior wall of the body. Some of them, however, pass in the opposite direction (figs. 51, 52) along the wall of the caecal prolongation of the metasome which contains the loop of the alimentary canal. Immediately on the dorsal side of the attachment of the stalk (fig. 126) the muscular layer is thick, and is not much broader than the diameter of the stalk. In passing dorsally (fig. 125) the layer broadens out so as to extend along at least a third of the circumference of the frontal section. The layer becomes considerably weaker as it approaches the collar, no doubt owing to the fact that some of the fibres successively insert themselves into the basement-membrane of the body-wall of the metasome. In *C. dodecalophus* in particular it is very obvious that the basement-membrane which lines the third body-cavity is specially thick in the region of this muscular layer.

When the dwindled remains of the muscles have arrived near the gill-slits (Pl. VI, fig. 69; Pl. XII, fig. 157) most of the fibres are left on the part of the body-wall which is anterior to the position of the external gill-pores, though a few of them pass behind these apertures. With the commencement of the collar-region (which in frontal sections is first seen on the ventral side of the mouth) the two coelomic sacs cease to constitute a median mesentery, and become widely separated from one another (fig. 124). They are then found as two triangular cavities, nearly filled with longitudinal muscle-fibres, and occupying a position immediately anterior to the gill-slits (figs. 68, 123, 156, *b. c.*^{3} *a.*). We are in fact dealing with two antero-ventral horns of the third body-cavity which extend forwards into the collar-region, in much the same way that the dorsal perihaemal cavities extend into the collar in Balanoglossus. The ventral horns

pass forwards as far as the region of the collar-canals (Pl. IV, fig. 41; Pl. VIII, fig. 93), and the last of the body-muscles are inserted into the septa which divide the ventral horns from the collar-cavity. I think there can be little doubt that none of the fibres traverse the septum; and indeed it may be stated that the longitudinal muscles in each of the segments of *Cephalodiscus* are restricted to that segment, just as the longitudinal muscles of Amphioxus or of a Fish are divided into myomeres by the myotomes or myocommata.

From the anterior border of septum $^{2}/_{3}$, in the immediate neighbourhood of the termination of the metasomatic muscles, originate the principal longitudinal muscles of the collar. These consist of a pair of strong bundles of fibres, the oral muscles (Pl. VIII, fig. 93; Pl. X, figs. 122—117, *or. m.*), which start from the region of the collar-canals, traversing the collar-cavity on either side of the mouth, and ending, to some extent at least, in septum $^{1}/_{2}$, opposite the origin of the radiating muscles which pass through the cavity of the proboscis. I point out below that these muscles are joined by fibres which have a different origin.

The arms themselves have a pair of longitudinal muscles, running along the basement-membrane of their morphologically inner side; that is to say, along the side of the arm-grooves; and a pair of weaker longitudinal muscles extending along their outer side (Pl. XII, fig. 141).

The principal muscles of the proboscis form two strong groups of fibres which diverge from the thick membrane which forms septum $^{1}/_{2}$, and are inserted largely into the basement-membrane of the anterior wall of the proboscis (Pl. XII, figs. 147—153, Pl. XI, figs. 137—139). These have already been described by M'Intosh (**87**) and Masterman (**97**, 2), both of whom have suggested that they enable the proboscis to be used as a sucker.

It will thus be seen that there is a functional continuity between the stalk-muscles and the longitudinal muscles of the anterior end of the animal. The contraction of this system will not only shorten the stalk (as is indicated by the numerous transverse wrinkles into which its wall is commonly thrown), but will also shorten the body, the collar as a whole, and its arms individually, and will retract the anterior body-wall of the proboscis. This general contraction is presumably associated with an attachment of the sucker-like base of the stalk to the wall of the coenoecium. The contractions are no doubt of importance, not only in the movements of the entire animal, but also of its separate parts. The movement of the proboscis, for instance, whether in crawling or in tube-building, must be largely controlled by the muscles which traverse its body-cavity.

The first two segments of *Cephalodiscus* probably have a mechanism similar to that of the tube-feet of an Echinoderm, contraction being effected by longitudinal muscles, and expansion by fluid pressure of its contents. It is impossible to avoid being struck by the fact that two of the principal sets of longitudinal muscles, namely those of the metasome and those of the collar, terminate in close connexion with the collar-canals. The probable action of these muscles on the collar-canals has been considered in describing those organs (p. 43).

The remainder of the muscles of *Cephalodiscus* appear to be associated with the coelomic epithelium, either of the body-wall or of the alimentary canal. The proboscis of *C. dodecalophus* is provided with a well developed layer of muscular fibres on its posterior wall (Fig. 151), the direction of which appears to differ according to the part of the proboscis which is examined.

Some of these fibres may be seen to leave the posterior wall from place to place, and to pass across the body-cavity to the anterior wall, where they are inserted into the basement-membrane. It appears to me that these muscles really form part of the system of radiating muscles which have already been noticed. The system originates from septum $^1/_2$, and while some of the fibres pass directly across the body-cavity to the opposite wall, others apply themselves closely to the posterior wall, along which they run for a certain distance, the fibres detaching themselves one by one and crossing the body-cavity to reach the anterior wall. The muscles under consideration accordingly radiate in all directions from the proboscis-stalk. Thus in a sagittal section of the proboscis passing at some distance from the median plane, the fibres near the middle of the posterior wall might be expected to be cut transversely, while they should become more and more oblique in approaching the two ends of the section. This appears to me to correspond with observed facts. I do not think that the anterior wall of the proboscis has any musculature independent of the fibres which reach it from the posterior wall.

The study of the buds (cf. Pl. XIII, figs. 176, 179, 181) seems to indicate that the morphologically anterior end of the proboscis is somewhere near the middle of the thick glandular epidermis of what I have termed the anterior side. If this be the case, the flattening of the organ is in an antero-posterior direction, and the radiating muscles may be described, in morphological terms, as a system of longitudinal muscles originating in the posterior half of the proboscis, and inserted into its anterior wall.

The collar is traversed, in most of its parts, by numerous fine fibrils, running as a rule perpendicularly across the body-cavity from one epithelium to the other. Each fibril is obviously nucleated at about the middle of its course (fig. 151). These fibrils are abundant in the operculum and along the whole length of the arms, except in the swollen tips which are characteristic of *C. dodecalophus*. It appears to me probable that they are contractile, and that they are responsible for most of the local alterations of fluid pressure which are so important for the effective working of the entire collar-system.

In addition to these fibrils, the collar contains numerous more definite muscle-fibres which form part of its body-wall. The principal group is constituted by the strong oral muscles. These have been partially described above, in discussing the functions they appear to perform in the movements of the collar-canals and in continuing the line of action of the body-musculature as far as the base of the proboscis. They are mentioned by Masterman (**97**, 2, p. 353, Pl. XXV, fig. 15) who states that in the mesodermic sheath of the pleurochords originate strong muscular bands which are inserted into septum $^1/_2$ opposite the origin of the radiating muscles of the proboscis. This, I think, is only part of the truth, the real facts being that the muscular band in question (on each side) is constituted by factors derived from various parts of the coelomic wall; and that while some of the fibres originate from the basement-membrane covering the mouth or pharynx, others start from septum $^2/_3$ and others again from the body-wall. Moreover it appears to me that the fibres which originate from the wall of the alimentary canal do not start from the pleurochords, but from a part of the basement-membrane which covers the ordinary epithelium lining the mouth and the commencement of the pharynx.

Fig. 93 (Pl. VIII) is a more or less sagittal section passing through one side of a neuter

zooid of *C. sibogae*, and it shews the greater part of the course of one of these muscles. The metasomatic musculature (*ms.*) is cut tangentially, and is seen to pass into the septum between the second and third body-cavities [1]). From the anterior side of this septum, in the immediate neighbourhood of the gill-slit (*g. s.*) and of the collar-canal (*c. c.*) starts the oral muscle (*or. m.*), which passes through the collar-cavity as far as septum $^1/_2$, into which some of its fibres appear to be inserted. The muscle receives, however, an important contribution of fibres from the oral side of the lower lip or operculum.

Fig. 107 (Pl. IX) is a part of a transverse section of *C. levinseni* which is favourably orientated for the study of part of the origin of the oral muscle. The section passes through the ventral side of the collar and metasome in such a way as to expose the surface of the basement-membrane (*b. m.*) belonging to the oral epidermis of the operculum, which is directed towards the proboscis. The section will be understood by referring to fig. 123, the bilobed portion of basement-membrane marked *b. m.* being that of the anterior wall of the epidermic recess at the base of the operculum. The muscle-fibres start from the ventral collar-mesentery and pass in a transverse direction across the wall of this recess, and in the same direction across the wall of the mouth (at the level *m.*), below the end of the recess. It may be noted, however, that the transverse fibres and the oblique fibres which are found on the anterior wall of septum $^2/_3$ are parts of a continuous layer. In suitably stained frontal sections similar to Pl. XII, fig. 156, the constituents of the oral muscle may be seen, cut transversely, in the angle of the collar-cavity on each side of the mouth, some in contact with the wall of the anterior horn of the third body-cavity and some in contact with the epithelium lining the mouth or with that of the oral surface of the operculum. Here they are continuous with the layer (not shewn in figs. 153—156) which occurs along the whole of the base of the epidermis of both surfaces of the operculum, and they are in fact merely a specialised part of this layer. Traced towards the dorsal surface (Figs. 154, 153) the oral muscle becomes more definite. In fig. 151, it is seen in sagittal section receiving fibres from the oral wall of the operculum, while in adjacent sections of the same specimen it receives other contributions from the basement-membrane covering the anterior wall of the mouth or of the commencement of the pharynx [2]).

The constitution of the oral muscle is thus complicated. It may be regarded as the principal muscular pillar of the proboscis, but its base is spread over a wide area, and some of its fibres probably act as an oral sphincter. The transverse course of the fibres on the ventral part of the operculum is doubtless of considerable functional importance if, as seems not improbable, particles of food pass into the opercular recess below the mouth before they are swallowed. The transverse course of the muscles here situated probably enables the opercular recess to empty itself by a sort of gulping action into the mouth.

It is difficult to arrive at complete certainty with regard to the course of the muscle-fibres in the operculum. In some parts, the fibres may be cut transversely in a sagittal section, while in others their course is more oblique. In the projecting lateral lobe of the operculum

1) It would hardly be possible from this section to prove that the septum divided the muscles of the two cavities; but the evidence of other specimens seems to me clear on this point.

2) It is not easy to say where the mouth ends and the pharynx begins.

the fibres of the oral surface run parallel to the free edge (fig. 148), while those of the outer wall cross them at right angles. The explanation of the course of the opercular muscles seems to me, however, much the same as that given for the proboscis; namely that the muscles are really a system of fibres which radiate out from the centre of the collar, the course of the fibres being differently modified on the two surfaces.

Thus the fibres of the oral side of the operculum sweep round the free border of the lateral lobe in a direction parallel to its free edge (fig. 148), while those of the aboral surface pass transversely outwards along the same region (fig. 149), and thus cross the other fibres at right angles. The extreme mobility of the operculum, of which there is excellent evidence in the varying positions assumed by this organ in preserved specimens, is doubtless due to the complicated course of the fibres of the musculature of its body-wall.

In accordance with what has already been said in a previous Section (p. 30) with regard to the morphology of the collar, both the operculum and the arms may be considered to be modifications of the free anterior edge of that region. The musculature of the arms is thus probably to be regarded as longitudinal. I am inclined to think that that of the operculum has really the same morphological direction, and that the actual course is the result of modifications of a longitudinal layer radiating out into what is practically a funnel-shaped edge formed by the arm-bases and the operculum. It is indeed not easy to explain the circularly disposed muscles seen in fig. 107 as longitudinal, since they appear to be in the line of the transverse circumference of the collar; but it must specially be noted that they seem to form part of the system of fibres seen on septum $^2/_3$. The main parts of the oral muscles again appear to have a circular or transverse direction, but their longitudinal character is perhaps indicated by the fact that some of their fibres pass from septum $^2/_3$ through the collar-cavity to septum $^1/_2$. In spite of these difficulties of interpretation, I am inclined to take the view, although with a good deal of hesitation, that the system of collar-muscles of *Cephalodiscus* is morphologically longitudinal. Some of the fibres can hardly be explained in any other way, and moreover I have been unable to obtain evidence that more than one layer is present at any point. It may thus possibly be the case that the entire somatic muscular system of *Cephalodiscus* is longitudinal.

In the arm-bases, there is a considerable development of muscular fibres in connexion with both the anterior and the posterior wall, although all the fibres are probably morphologically longitudinal. There is clear evidence that numerous fibres run across the coelom from one wall to the other, as represented in figs. 147—149. These fibres have definitely the character of muscle-fibres, as judged by their staining properties, and they appear to differ histologically from the delicate nucleated filaments which cross the cavity of the operculum. At the origin of the arms, the fibres have a complicated course, and there is a good deal of crossing of the fibres which traverse the collar-cavity in different directions.

The arms themselves (fig. 141, *5*, *6*) are provided with a strong layer of longitudinal muscular fibres, on each side of the middle line, runing along the whole of the anterior, grooved surface, and with a similar, but somewhat weaker, layer on each side of their dorsal surface, continuous with the muscles of the dorsal or posterior wall of the arm-bases.

The entire wall of the pharynx and oesophagus, so far as it is exposed to the body-cavities, whether of the collar or of the trunk, possesses a single layer of fibres. I have never observed the slightest indication of any crossing of fibres, although the muscular system can be seen with great clearness in sections stained with iron-haematoxylin, particularly where parts of the wall of the alimentary canal are cut tangentially, as in fig. 151. It need hardly be pointed out that where sacculations of the wall occur, the direction of the fibres may appear to change; but their real course seems to me to be exclusively longitudinal. The pleurochords of MASTERMAN are in no way different from other parts of the pharyngeal epithelium, so far as the muscular layer is concerned. But when the region of a gill-slit is reached, the fibres take a sphincter-like course round the posterior or external wall of the tube leading to the external gill-pore. These sphincter-like fibres are a direct continuation of the longitudinal fibres on the part of the pharynx which is nearer the stomach, and of the longitudinal muscles of the body-wall of the trunk. On the anterior or median border of the gill-slit, the fibres contained in the anterior horn of the third body-cavity (fig. 156, *b.c.*^{3}*a.*) no doubt assist in the closure of the gill-pore.

I have not noticed any differences of importance between the muscular systems of different species of *Cephalodiscus*, except so far as has already been pointed out in describing the stalk. The neuter individuals of *C. sibogae* are, however, provided with muscles which seem to be specially strong in proportion to the size of the animal.

XIII. NERVOUS SYSTEM.

In 1887 I was able to shew that the nervous system of *Cephalodiscus* conformed to the type found in Balanoglossus. Since then, more detailed accounts have been given by MASTERMAN (**97**, 2; **98**, 2; **03**), many of whose results I am able to confirm.

MASTERMAN (**97**, 2, p. 342) recognises the following parts of the nervous system of *Cephalodiscus*: (I) the central nervous system; (II) its backward continuation as the lateral nerves, which are prolonged down the body as (III) a pair of lateral nerves similar to those of *Phoronis*; (IV) a post-oral ring given off from (II) at the posterior edge of the collar, and becoming lost ventrally in the operculum, over which it forms a nerve-layer, (V) a broad tract lying beneath the thickened anterior ectoderm of the proboscis, and connected with the central nervous system round the "apex" or dorsal margin of that structure, (VI) a "pre-oral nerve" passing ventrally along the posterior wall of the proboscis and originating from the anterior part of the central nervous system by a root on each side; (VII) "several nerve-fibres" which run down the anterior surface of the metasome, some of them being continued into the nerves of the stalk; (VIII) the nerves to the arms.

In a later account (**98**, 2, p. 513) MASTERMAN substitutes for (VII) "a broad nervous tract", which passes down the ventral line of the body into the stalk, while he states that the lateral nerves (III) also extend into the stalk.

There can be no question of the nervous nature of the parts numbered (I), (II), (VII),

and (VIII) in the above list. (V) is, I think, almost equally certain; and, as MASTERMAN states, it lies at the base of the glandular epithelium of the proboscis (Pl. IV, figs. 36, 42). I have not been able to trace it with complete certainty round the dorsal or lateral margins of the proboscis, although figs. 151—146 (Pl. XII) appear to indicate that this is really its mode of connexion with the central nervous system. I think that MASTERMAN is right in describing the operculum as being supplied with a nerve-layer, although I have not indicated it in most of my figures, and I am not certain of its communications with other parts of the nervous system. But it may be remarked that *Cephalodiscus* resembles Balanoglossus in possessing a general nerve-plexus in its epidermis, and that it is only the thicker parts of that plexus which can be recognised as definite nerve-tracts. It might be going too far to say that the plexus is universal in *Cephalodiscus*, but it is certainly present in many of the thicker parts of the epidermis, while its existence is further indicated by the fact that the nerve-tracts commonly fade away gradually at their edges.

The following account of the nervous system, which is based on my own observations, besides giving a general account of the whole system, refers specially to the parts described by MASTERMAN and numbered (III), (VI) and (VII) in the above list.

The nervous system of *Cephalodiscus* is very strongly developed, and I emphasize this fact because it has recently been asserted by DE SELYS LONGCHAMPS (**04**, p. 113) that it is "peu développé" or even "rudimentaire". This is very far from being the case, the central nervous system in particular consisting of a large mass of nerve-tissue. It has been pointed out by MORGAN (**94**, p. 72) that in retaining its central nervous system in the outer epidermis, *Cephalodiscus* must be regarded as more archaic than its relation Balanoglossus.

The central nervous system has essentially the same characters in all the species, even the curiously reduced male individuals of *C. sibogae* forming no exception to this statement. It gives rise to a great thickening of the epidermis in the dorsal region of the collar, extending thence on to the posterior part of the proboscis. It is shewn in more or less sagittal sections in Pl. IV, figs. 42, 41 *(C. dodecalophus)*, figs. 34—36 *(C. levinseni)*, fig. 37 *(C. gracilis)*, Pl. VIII, fig. 93 (*C. sibogae*, neuter) and Pl. VII, fig. 79 (*C. sibogae*, male); while Pl. X, figs. 112—118, referring to *C. levinseni*, illustrate its relations as seen in frontal sections. The greater part of the nervous mass consists of a conspicuous layer of fibrillar material, resting on the basement-membrane; while ganglion-cells may be clearly distinguished, in certain parts of the organ, among the bases of the epithelial ectoderm-cells. Thus in the original of fig. 42, some half-dozen ganglion cells occupy the epidermic swelling which in the figure appears to project into the mass of fibrils near the posterior end of the brain.

In his latest paper on *Cephalodiscus* (**03**, p. 717) MASTERMAN describes what he terms the "ectodermal pit", a crescentic groove running transversely across the region of the central nervous system, and representing the line of division between the proboscis and the collar. The proboscis-pores are said to open at the outer ends of the crescent. I have on various occasions noticed transverse grooves corresponding to the "ectodermal pit", but I think that MASTERMAN is wrong in describing it as a definite structure. It appears to me to be the result of the varying positions of the anterior end of the body and of the varying states of contraction

of the muscles. In other words, the "ectodermal pit" is simply a temporary crumple of the skin, without any constant relation to the proboscis-pores. Thus fig. 42 shews no definite trace of the structure, while in figs. 149, 150 (Pl. XII) it appears to be well developed. But in fig. 151, from the same series, the outer end of the groove is seen opposite the notochord (*nch.*), while the proboscis-pore (*p. p. l.*) opens at some distance in front of the groove; and the same relations are already indicated in fig. 150.

The proboscis-pores (Pl. X, fig. 112; Pl. XI, figs. 137, 138; Pl. XII, fig. 158; *p. p.*) traverse the central nervous system at a level which is indicated by the position of the pericardium and the anterior dorsal horns of the collar-cavity. I have not certainly found them in the males of *C. sibogae*, but their number and position are, except for this doubtful case, invariable.

The strong nerves to the arms are direct lateral continuations of the central nervous system. They are seen in the sagittal sections represented in figs. 149—141 (Pl. XII), and in the frontal sections shewn in figs. 113—118 (Pl. X). The arm-nerve lies at the base of the dorsal epidermis, which is often triangular in transverse section (figs. 141, 142).

The nerve-layer at the base of the glandular epithelium of the proboscis is shewn in Pl. IV, figs. 36, 42, and elsewhere.

The part of the central nervous system which extends on to the dorsal side of the proboscis is connected with nerve-tracts running in a ventral direction along the posterior wall of that organ. In *C. dodecalophus* I have been able to recognise two lateral tracts and a median tract (Pl. XII, figs. 152—155) which appear to correspond with MASTERMAN's "pre-oral nerves".

The central nervous system as seen in a median sagittal section (Pl. IV, figs. 34, 42) comes to an abrupt termination posteriorly at a point which corresponds with the hind edge of the collar. On either side of the middle line it passes into the strong "lateral nerves" described by MASTERMAN (**97**, 2, p. 342; **98**, 2, p. 513), with whom I do not, however, altogether agree as to their further course, since I have been unable to recognise the independence of the two nerves which in the diagram given by MASTERMAN in his later paper (**98**, Pl. V, fig. 85) are supposed to run, on each side of the body, from the posterior end of the nervous system to the stalk. According to my own results, there is on each side a single lateral nerve, which is an extremely conspicuous structure passing from the central nervous system in the lateral ectoderm.

In the first part of its course the lateral nerve is in contact with the basement-membrane belonging both to the collar-cavity and to the metasomatic cavity. This is seen in Pl. XII, fig. 150 (*l. n.*); while in fig. 151, a section of the same individual slightly nearer the middle line, the lateral nerve is separated by parts of the pharynx and body-cavity from the central nervous system, still retaining its position adjacent to both the second and the third body-cavity.

Fig. 152 is a frontal section which passes somewhat ventrally to the central nervous system, and therefore cuts the lateral nerves near their origin. The subsequent sections (figs. 153—155) shew that the nerves pass behind the collar-canals, with which they are in contact. On reaching the level of the gill-slits (fig. 156), behind which they lie, they are found to have lost all

connexion with the collar and to have passed entirely into the metasome. It is thus hardly correct to speak of them as passing in the posterior part of the collar along the whole of their course to the ventral surface. MASTERMAN considers that these nerves extend along the body laterally, and he definitely compares them with the lateral nerves of *Phoronis*. This is presumably illustrated by fig. 17 of his paper published in 1897 (2). My own observations indicate that the lateral nerves pass ventrally into the strong nerve-plexus which is seen on the anterior side of the body in sagittal sections (Pl. IV, fig. 42 and Pl. XIII, fig. 181). MASTERMAN's figure, to which I have just alluded, shews the nerves correctly, but sections taken nearer the stalk would probably have indicated that the paired nerves pass into an unpaired anterior nerve-tract. In favourable specimens this course can be distinctly made out, although it is not always easy to demonstrate it in specimens in which the epidermis is much stretched, and it is accordingly not shewn in all my figures passing through the region in question. Figs. 119—124 (Pl. X) shew the lateral nerves, in frontal sections of *C. levinseni*. They differ in no essential respect from the corresponding structures in *C. dodecalophus*. Fig. 124, immediately ventral to the region of the gill-slits, shews the ventral body-musculature along a considerable part of the anterior surface. The lateral nerves have reached the posterior borders of the muscular areas. In the next section figured (fig. 125) the nerve-layer is not so conspicuous as to be demonstrative, and it is accordingly not represented in the drawing. But in similar sections of *C. dodecalophus* it may be seen that the lateral nerves, after acquiring the position shewn in fig. 124, spread out rapidly over the whole of the area of the antero-ventral musculature and become continuous with the strong stalk-nerves shewn in fig. 133. The sagittal sections (fig. 181) demonstrate the existence of a large nerve-plexus along the anterior side of the body from a region not far behind the gill-slits to the stalk.

The function of the lateral nerves is thus to place the musculature of the metasome in direct communication with the central nervous system, a conclusion which is in accordance with the great development of these nerve-tracts.

C. gracilis and *C. sibogae* are less favourable for the examination of the nervous system than the other two species, in consequence of their less robust structure. The main features of the nervous system, as above described, can, however, be recognised in these species, and I am not able to point out any differences of importance.

It is a point of special interest that the reduced male individuals of *C. sibogae* (figs. 79, 81—84) have a well developed central nervous system, indicating that they must be regarded as more than mere reproductive appendages of the colony. The development of the nervous system is perhaps principally correlated with the functions of the proboscis and of the pair of arms.

XIV. VASCULAR SYSTEM.

The credit of discovering this system in *Cephalodiscus* belongs to MASTERMAN, who in his first account (**97**, 2, p. 350), described the following parts: — (I) a large cavity beneath

the central nervous system, which he has more recently admitted (**99**, 2, pp. 359, 361) not to be a blood-space, but to have the peculiar relation to the vascular system possessed by the pericardium of Balanoglossus, as described by SPENGEL; (II) a vessel proceeding backwards from the pericardium in the dorsal mesentery of the collar, bifurcating at the anterior border of the dorsal diverticulum of the pharynx, and reuniting behind that cavity to form (III) a vessel lying in the mesentery between the pharynx and the rectum, connected with (IV) a system of sinuses round the stomach; (V) vessels to the ovaries; (VI) a ventral vessel, passing down the anterior side of the body and stalk; and (VII) a vessel on the dorsal side of the body-cavity of each arm, giving off a branch to each tentacle. In a later paper (**98**, 2, p. 512, figs. 12, 13) MASTERMAN gives figures shewing that the ovaries are supplied from the dorsal blood-vessel, and in the same memoir (p. 513) he describes a "dorsal" and "ventral" vessel in the stalk, which he states to be "direct continuations of the similar vessels in the trunk".

Still more recently (**03**, p. 719), MASTERMAN gives a more elaborate account of the vascular system of the "central complex", or region between the buccal shield and the mouth. The general result of this paper is to indicate an almost complete resemblance between Balanoglossus and *Cephalodiscus* in the details of the vascular system of the proboscis-stalk. The blood-sinus which runs in the dorsal collar-mesentery communicates with the "heart", which is related to the pericardium in the same way as in Balanoglossus. Glomeruli are described, both on the anterior wall of the pericardium and on the "ventral blood-sinus" which lies beneath the notochord. There is a blood-sinus coming from the dorsal wall of the proboscis to the anterior glomerulus; and vessels passing from the arms are said to enter the dorsal sinus at the level of the posterior end of the pericardium. The ventral sinus extends backwards as far as the base of the notochord, where it divides into two vessels which pass round the mouth.

I have no wish to dispute the accuracy of most of MASTERMAN's statements with regard to the vascular system, although on one or two points I cannot agree with him. But I must admit that I have not been able to satisfy myself of the existence of all the vessels which he describes.

The question really turns on the interpretation which should be given to certain spaces in *Cephalodiscus* which may be vascular and on the other hand may be merely artefacts. There is of course no trace of colour in the blood of the preserved specimens, nor are any corpuscles to be seen. Certain evidence of the presence of a coagulum inside the "vessels" can only rarely be obtained. There are, however, in *Cephalodiscus*, numerous spaces between the limiting membranes of adjacent coelomic spaces, or between the membrane and the ectoderm or endoderm; and these spaces may be vascular in nature. But when one remembers the fact that the material which is at present forthcoming was not preserved by refined histological methods, and further that there is evidence of great contraction in certain parts of the animal, I think it is well to be cautious in assuming that all the spaces in question are vascular.

I am none the less inclined to think that most of MASTERMAN's account is substantially accurate. I cannot agree with his statement referred to above that the "dorsal" and "ventral" vessels of the stalk are "direct continuations" of the "similar vessels in the trunk". This appears

to me correct for the "ventral" or anterior vessel; but a moment's consideration will shew that it would be impossible for the median "dorsal" vessel of the stalk to be a direct continuation of the dorsal vessel of the body unless it could traverse, or pass to one side of, the second stomach and intestine. Nor can I agree with the statement that each tentacle has a vessel on the dorsal side of its coelomic cavity. It is easy to find appearances similar to those shewn by MASTERMAN (**97**, 2, Plate XXVI, fig. 27). With certain methods of staining the crescentic area seen in the transverse section appears to be hollow. But in other cases it seems to be clear that the crescentic appearance is simply due to a thickening of the basement-membrane lining the coelomic cavity; and I believe that MASTERMAN's tentacle-vessels are in fact merely skeletal thickenings of that membrane.

My own results on the "vascular system" of *Cephalodiscus* may be considered under two heads: — (1) those spaces whose vascular nature is practically certain, and (2) those with regard to which some caution in interpretation seems to be desirable.

(1) Under the heading of spaces the vascular nature of which is practically certain, I include the vessel which lies in the dorsal mesentery of the metasome, adjacent to the wall of the pharynx; the vessels given off from this to the reproductive organs; the two vessels of the stalk, and their continuations in the body; and lastly the "heart", or pericardial sinus, which is invaginated into the posterior wall of the pericardium. All these parts have been described by MASTERMAN in one or other of his accounts. Under the heading (2) of spaces with regard to whose interpretation as vessels it is well to exercise some caution I include practically all the other "vessels" described by MASTERMAN.

Dorsal vessel.

This name may be employed for the vessel which is contained in the dorsal mesentery of the metasome. Evidence of its existence can be obtained in most specimens of *Cephalodiscus*. In those in which the vessel has been preserved in a dilated condition it forms an extremely conspicuous organ, and it is in fact far the largest vessel in the animal.

The dorsal vessel (*d.v.*) is shewn in the combined sagittal section of *C. gracilis* (Pl. IV, fig. 37), in the actual sagittal sections (Pl. V, figs. 43—46) and in the frontal sections (Pl. VI, figs. 67—70) of the same species. Pl. III, fig. 22, reconstructed from the series of sagittal sections by the ground glass method, shews this vessel as a large cylindrical space which starts from the anterior caecal projection of the stomach, and then passes in an obliquely dorsal direction in such a way as to lie, in the whole of its course, parallel to the dorsal wall of the pharynx. The vessel is also conspicuous in the sagittal section (fig. 33) of *C. levinseni*, where it has the same relations. It is shewn in transverse section (Pl. XII, figs. 152—157) in *C. dodecalophus*, and lastly it is clearly seen in both neuter (Pl. VIII, figs. 90, 91) and male individuals (figs. 86—88) of *C. sibogae*. The vessel in question is particularly clear in the male individual represented in figs. 86—88, and in this case, as I have also observed in the neuter of the same species, it contains an obvious coagulum. The walls of the vessel are usually very thin, although in *C. levinseni* (fig. 33) it appears to be fairly thick. I have not been able to demonstrate any system of muscles connected with its wall, although I am not sure that they

are absent. It is not improbable, however, that it functions as a reservoir of blood derived from the walls of the stomach. The movement of the blood in the vessel might well be effected by the pressure of the coelomic fluid induced by contractions of the body-wall.

There can thus be no question that the dorsal vessel is an important structure in *Cephalodiscus*. Examining its ventral end (figs. 33, 37) it is found to end abruptly on the surface of the dorsal caecum of the stomach. In most cases I cannot certainly demonstrate any vessels entering it from the stomach; but the evidence of the bud shewn in Pl. V, figs. 57, 58 is in favour of the view that it receives its blood from a system of sinuses lying between the gastric epithelium and the limiting membrane of the body-cavity.

Vessels of the gonads.

Near its dorsal end, the dorsal mesentery gives off a pair of lateral mesenteries (figs. 120—123, *ov. m.*) which are inserted into the entire length of the oviducts in the female, and into the dorsal part of the internal walls of the ovaries. Each lateral mesentery carries a conspicuous vessel (Pl. XII, fig. 151; Pl. V, fig. 45, *ov. v.*) which passes to the wall of the ovary, somewhat ventrally to the internal end of its pigmented duct. The large amount of yolk deposited in the eggs of *Cephalodiscus* implies an abundant nutriment supplied to the ovaries; and I think it may thus fairly be inferred that the blood passes from the wall of the stomach in a dorsal direction to supply the ovaries. In the male *C. sibogae*, a similar arrangement obtains. The dorsal vessel (Pl. VIII, figs. 87, 86) extends from the dorsal surface of the bend of the vestigial alimentary canal to the dorsal ends of the testes, which are supplied by large vessels passing along paths which may be regarded as lateral mesenteries homologous with those of the ovaries. The vestigial character of the alimentary canal in the male offers, however, some difficulty as to the source of the nutritive fluid contained in the vessel. This question will be considered under the heading of the male *C. sibogae* (p. 88).

Vessels of the stalk.

These vessels occur in the position already described by MASTERMAN, on what he terms the "ventral" and "dorsal" sides of the stalk respectively. In view of the orientation adopted in this Report, according to which the entire stalk is a ventral appendage of the body, I prefer to call the vessels respectively "anterior" and "posterior", and to regard them as two limbs of a loop-like ventral vessel which extends into the stalk. The continuity of the two vessels at the basal end of the stalk has not however, been demonstrated with certainty.

The vessels are seen in transverse section, in *C. dodecalophus* (Pl. XI, fig. 133), as small dilatations of the two ridges of basement-membrane which alone represent the ventral mesentery of the stalk. It may be supposed that primitively the ventral mesentery extended as a complete partition down the stalk. With the filling up of its cavity which this organ has for the most part undergone by the development of the longitudinal muscles and their investing connective tissue, the ventral mesentery has persisted as a distinct structure at the anterior and posterior sides only.

The condition of the stalk-vessels is probably not quite simple at the basal extremity

of the stalk. It is complicated by the development of the buds, which, as MASTERMAN has shewn (**98**, 2, p. 515) receive branches from one of the stalk-vessels. There is some evidence in *C. sibogae* that the two vessels communicate by means of a plexus at the basal end of the stalk; but whether the connexion is usually of this nature, or whether, as some sections seem to indicate, the two vessels form a simple loop at the base of the stalk, it is probable that they may be regarded as respectively afferent and efferent in function.

The anterior vessel passes from the stalk along the anterior part of the ventral mesentery of the body (figs. 29, 126, 125, *a.v.*, *a.v.*[1]), where it lies close to the body-wall; and in suitable specimens it can be distinctly traced as far as septum $^1/_2$. The posterior vessel, on entering the body, passes in the ventral mesentery as far as the wall of the alimentary canal. In *C. gracilis* (Pl. VI, fig. 71, Pl. V, fig. 53, and the reconstruction Pl. III, fig. 22) it ends on the surface of the second stomach as a distinct dilatation, the structure of which cannot clearly be made out, although in one specimen the dilatation has been observed to receive muscle-fibres from the longitudinal layer of the anterior wall of the metasome. The ending of the posterior stalk-vessel on the second stomach is also somewhat dilated in *C. dodecalophus* (Pl. XIII, fig. 169).

The clearest proof that the structures here described as vessels are really of that nature is obtained from *C. gracilis*. The stalk-vessels are here unusually large (figs. 28, 29, 134, 135); and although they are commonly displaced so as to take up a lateral position, a careful examination of the stalk usually serves to shew that they are connected respectively with its anterior and posterior walls. The connexion is, however, far less obvious than in *C. dodecalophus* and *C. levinseni*, since remains of the ventral mesentery connecting the vessels with the body-wall are not easily discovered. The vessels are large, thin-walled cavities lying internally to the muscular layer, in the sparse connective tissue which occupies the central part of the stalk in this species.

The stalk-vessels of *C. gracilis* are sometimes very conspicuous in entire preparations of young buds. They are shewn in Pl. III, figs. 28, 29; and in this specimen it could be proved that the posterior vessel becomes attached to the wall of the alimentary canal of the bud, while the anterior vessel passes along the inner side of the median line of the anterior wall of the body.

Attention may here be called to the account which has recently been given by FOWLER (**04**, p. 23) of the structure of *Rhabdopleura*. The resemblance between the stalk, as described by FOWLER, and the stalk of *Cephalodiscus* is practically complete, both as regards mode of origin and minute structure. FOWLER's fig. 2 might stand for the stalk of *C. levinseni* almost as well as for that of *Rhabdopleura*, the completeness of the mesentery and the difference in size excepted. It shews a triangular ventral or anterior thickening of the epidermis which has "very much the appearance of a superficial nerve". The longitudinal muscles are related to those of the body exactly as in *Cephalodiscus*. The cavity of the stalk is divided by a median mesentery, in which run two canals. The one next the nerve (*b*) was not found in all specimens, but the one (*end?*) which occurs at the middle of the mesentery is always present and is "generally completely filled with a granular mass".

I think there can be no doubt that these two cavities are the homologues of what MASTERMAN has described as the stalk-vessels of *Cephalodiscus*, and indeed FOWLER admits that

homology. He is apparently induced to reject MASTERMAN's interpretation by finding that the central or posterior tube of the stalk is "continuous with the lining of the alimentary canal". The proof of this last statement is not given by FOWLER, and I think it more probable that the relation of the posterior tube to the alimentary canal is of the kind indicated in figs. 22 and 71 for *C. gracilis*. FOWLER supposes that the central tube is endodermic, and I imagine that his view of the budding is that it behaves in somewhat the same way as the epicardium of a Tunicate. But there is no evidence that this is the case, and the account given by MASTERMAN (**98**, 2) of the budding of *Cephalodiscus* is distinctly opposed to FOWLER's view. There can be little doubt that the same interpretation of the structures in question applies to the two genera; and it appears to me probable that in both cases the stalk is provided with an anterior and a posterior limb of a loop-like ventral vessel, the posterior limb terminating on the wall of the alimentary canal.

Pericardial sinus or heart.

The pericardium and pericardial sinus form a conspicuous feature of all specimens that are sufficiently well preserved. The pericardium (*per.*) has precisely the same relations as those of the same organ in Balanoglossus (the "Herzblase") as described by SPENGEL (**93**, p. 505). It is well shewn in MASTERMAN's most recent paper (**03**, figs. 1—8), and is illustrated by Pl. XIII, figs. 181, 182, 173; Pl. XI, fig. 138, Pl. IV, figs. 33, 37 of the present Report. It is in contact with the tip of the notochord (fig. 33) and lies immediately beneath the central nervous system. The proboscis-pores open into the anterior body-cavity between its lateral walls and the dorsal horns of the collar-cavity (figs. 112, 137, 138). The posterior wall of the pericardium is invaginated, the space thus formed (heart) having the same relation to the pericardium that is found in the Tunicata (cf. RITTER, **02**, 1). SPENGEL (**93**, pp. 506, 625) has given reasons for believing that in Balanoglossus the pericardium, although not in itself a vascular space, may be regarded as functionally a part of the vascular system, since the blood in the heart is propelled by the rhythmical contractions of the pericardium — contractions which are well known to occur in Tornaria. The identity of the relations of the pericardium to other organs in Enteropneusta and *Cephalodiscus* makes it highly probable that what is true of the former is also true of the latter.

The pericardium in *Cephalodiscus* is developed at a very early stage in the buds, and is further considered in Section XVI.

I come now to those parts of the vascular system which I regard as less certainly proved to exist. Among these are the "vessels" described by MASTERMAN in the immediate neighbourhood of the pericardium and notochord. I do not feel myself in a position either to assert or to deny the existence of these vessels, though I regard it as highly probable, on *a priori* grounds, that they do exist. I have indicated above (p. 74) the general nature of MASTERMAN's results with regard to these particular vessels.

Although I have devoted a considerable amount of attention to the region in which the dorsal vessel terminates in front, I have found but little evidence which appears to me

demonstrative. In many cases I can obtain no proof that the vessel in question supplies any organs other than the gonads. In the sections of *C. levinseni* shewn in Pl. X, however, there is evidence that the vessel is prolonged as far as the dorsal side of the dorsal diverticulum of the pharynx at least (fig. 119). In several sections through the collar-region I find spaces similar to the triangular space at the dorsal root of the collar-mesentery in figs. 114, 115, or in other positions between the central nervous system and the limiting membrane of the collar. Some of these spaces have very much the appearance of being artefacts (and indeed I have not represented them in all the figures), but it is not impossible that they may be normal structures. In MASTERMAN's original account of the vascular system (**97**, 2, figs. 7, 8) the main vessel of the collar is represented as occupying the entire height of the mesentery, and in fact as being a space between the two collar-cavities, whose limiting membranes do not actually meet at any point. In most cases I can obtain no certain evidence that the collar-mesentery has this double character.

In several of the sections of *C. levinseni* I find evidence of the existence of a finer membrane internally to the principal limiting membrane of the collar (figs. 116—118). The latter is thick and is in immediate contact with the epidermis, by which it has presumably been secreted. The inner membrane is much thinner, and there seems reason to believe that it constitutes that part of the limiting membrane ("Grenzmembran" in SPENGEL's sense) which is derived from the coelomic epithelium. It is by no means impossible that the spaces between these two layers of the limiting membrane are vascular in character.

The peritoneum is often not in contact with the outer surface of the epithelium of the alimentary canal. Some of the spaces thus constituted are almost certainly due to defective preservation, but I regard it as highly probable that splanchnic sinuses do occur, externally to the alimentary epithelium. Perhaps the most constant of these spaces is a large oral sinus (?) which I find passing from the sides to the ventral aspect of the mouth in *C. levinseni* (Pl. X, figs. 121—124, *or. s.*).

Although I fully admit the unsatisfactory nature of the evidence with regard to the peripheral vessels of *Cephalodiscus*, it may be worth while to attempt to form some idea of the probable nature of the circulation in this animal.

The cardinal fact with which it appears to me justifiable to start is the large size of the main dorsal vessel which connects the stomach with the reproductive organs. It is highly probable that this is a nutritive arrangement, in which case it may be inferred that the blood is collected from sinuses which lie on the surface of the stomach (as appears to be indicated by Pl. V, figs. 57, 58) and that it then passes forwards through the dorsal vessel to supply the ovaries. I have no evidence with regard to the efferent vessels of the ovaries; but it is conceivable that these might pass to the skin along the oviducts.

If MASTERMAN is correct in his account of the vessels of the "central complex", it is probable that that portion of the blood which does not enter the ovaries continues its course along the dorsal side of the alimentary canal and is carried by the sinus in the dorsal collar mesentery, as far as the heart. Here the circulation is presumably reinforced by the contractions

of the pericardium, which would propel the blood through the glomeruli and along MASTERMAN's ventral sinus (which is said to underlie the notochord) to the front border of the mouth, travelling round the sides of the mouth through the two vessels described in that position by MASTERMAN. These may be continuous with the oral sinus of which I have obtained some evidence in *C. levinseni*. The course of the blood, as thus suggested, would be in agreement with the course which has been described by SPENGEL in Balanoglossus.

The anterior ventral vessel of the body and stalk can be traced as far as the septum between the second and third body-cavities, or in one case (*C. levinseni*, Pl. X, fig. 124) even into the incomplete ventral mesentery of the collar. It appears to me probable that this ventral vessel in some way receives a part at least of the blood coming from the collar, and conveys it to the stalk by the vessel running on the anterior side of this structure. After having traversed the entire length of the stalk, it may be supposed that the blood returns by the posterior stalk-vessel to the wall of the second stomach where, in *C. gracilis* at least (figs. 22, 71) it appears to end in a dilated structure which is probably muscular. This may have the function of propelling the blood through the sinuses of the stomach and so of enabling it to reach the origin of the dorsal vessel. It is, however, possible that it acts in exactly the opposite direction, and that the posterior vessel is the afferent vessel of the stalk.

If there be anything in this entirely tentative scheme of the circulation it may be noted that the force of the beat of the pericardium would appear to be largely of importance in driving the blood through the stalk. In the long-stalked forms (*C. gracilis* and *C. sibogae*) there must be a considerable amount of resistance to be overcome in this region; and it may further be remembered that the stalk requires an efficient nutritive arrangement, not only to supply its strongly developed muscles, but also for the growth of the buds which are produced so profusely from the basal end of the stalk in these species.

XV. REPRODUCTIVE ORGANS.

The zooids of *C. dodecalophus* appear to be without exception female. As all the previous literature of the genus refers to this species, it follows that the male organs have not hitherto been described, although I have alluded to the males of *C. sibogae* in Vol. VII of "The Cambridge Natural History" (**04**, p. 26). The only previous accounts of the male organs of the Pterobranchia refer to *Rhabdopleura*, and are represented by LANKESTER's observation (**84**, p. 633) that a single testis occurs on the right [1]) side of the intestine, opening to the exterior near the anus, its blind end in some cases projecting beyond the part of the body-wall which contains the loop of the alimentary canal; and by the remarkable statements of CONTE and VANEY (**02**, 1), to which I shall refer later.

The material at present under consideration consists of female colonies of *C. dodecalophus*, *C. levinseni* and *C. gracilis* and a male colony of *C. sibogae*.

1) LANKESTER's fig. 7 (Pl. XL) shews the testis on the left side, as indicated in the explanation of the Plates (p. 645). The figure is perhaps reversed.

Female organs.

In the three species represented by female colonies it is probably not too much to say that all the adult zooids without exception possess a pair of ovaries. These make their appearance at an early stage in the budding, so that it is really only the very young buds in which gonads cannot be detected.

The ovaries are a pair of organs, symmetrically disposed on either side of the middle line, and they occur in the dorsal part of the third body-cavity, between the anus and the pharynx. The major part of the organ is composed of an ovoid mass containing the eggs. In adult specimens it is usual to find that in addition to a number of immature eggs the ovary contains a single egg in which a large quantity of yolk has made its appearance. The ripe ovarian egg thus reaches a large size (as much as 380 μ. in length in *C. gracilis*), and in an individual which contains a ripe egg there is commonly some asymmetry of the two ovaries, one of which may be much smaller than the other owing to the fact that it contains no ripe egg. In favourable specimens, there is an indication of a central cavity in the ovary; and the organ appears to be a hollow sac, the lining epithelium of which gives rise to the eggs. The ripe egg occupies the ventral part of the ovary (fig. 42), while the remains of the germinal epithelium are at the base of the oviduct.

The oviducts are one of the most characteristic features of *Cephalodiscus*. Their wall contains a pigment which is not dissolved by spirit, and the oviducts are thus so readily seen through the thin body-wall that they were originally described as eyes. The oviduct is a tubular prolongation of the cavity of the ovary. The external apertures are situated on the dorsal swelling of the metasome which immediately succeeds the central nervous system.

The frontal sections of *C. levinseni* represented on Plate X will serve to explain the relations of the ovaries and their external apertures. On reaching the posterior end of the collar (fig. 118) the dorsal projection of the metasome first makes its appearance as a longitudinal ridge of body-wall attached to the dorsal side of the collar. The two collar-cavities are here separated from one another by the dorsal diverticulum of the pharynx (*div.*), and between this and the central nervous system is seen the extreme tip of the right third body-cavity (*b. c.*[3]). The longitudinal ridge of body-wall separates from one another the entrances to two deep recesses lined by the epidermis of the metasome, and bounded in front by the part of the collar-wall which contains the lateral nerve-tract passing from the central nervous system to the stalk. This is shewn, on the left side, in fig. 119, while in fig. 120 it will be seen that the same oviduct opens into the posterior side of this recess. On the right side of fig. 120 the recess is already passed, and the oviduct is no longer connected with the body-wall. The part of the body which contains the oviducts is marked by a conspicuous dorsal furrow (figs. 119—122). Each oviduct is supported by a lateral or ovarian mesentery, which reaches the body-wall dorsally (figs. 119, 120), while more ventrally it leaves the body-wall and passes along the dorsal mesentery of the metasome to the dorsal vessel. In the region of the external opening of the oviduct the ovarian mesentery passes from the body-wall, near the middle line, to the oviduct in such a way as to appear to cut off a posterior section of the third body-cavity (figs. 119, 120); but in later sections in which the oviduct has relinquished its connexion with

the body-wall, this division is in free communication with the remainder of the cavity round the posterior wall of the oviduct (figs. 121, 122). At the ventral ends of the oviducts, the mesenteries of these organs originate from near the middle of the median mesentery (fig. 122). The ovarian mesenteries are continued as far as at the extreme dorsal ends of the ovaries (fig. 123), which along the greater part of their course are not supported by mesenteries (figs. 124, 125). In zooids in which ripe eggs are not being produced, the ovary and oviduct lie in the same straight line. This is seen in fig. 33, in which the right ovary is shewn, on the far side of the large dorsal vessel. The wall of the epidermic recess into which the oviduct opens is seen as an ovoid mass of cells which carries the pigmented oviduct to some little distance from the level of the median part of the dorsal body-wall. In zooids containing ripe eggs, the dorsal part of the ovary may be considerably bent, as shewn in fig. 139 (Pl. XI).

The relations of the ovaries and oviducts of *C. dodecalophus* are essentially similar to those found in *C. levinseni*. Fig. 42 shews an old ovary, bent in the way just referred to in the other species. The ovarian mesenteries are shewn, in frontal sections, in figs. 152—156, while fig. 157 demonstrates the absence of the mesenteries in the more ventral parts of the ovaries. Fig. 151 illustrates the position of the mesenteries as seen in an obliquely longitudinal section, which passes mostly through the right side of the animal, but also shews some of the organs of the left side. The edge of the right oviduct (*ovd. r.*) is just cut, while the right ovarian mesentery (*ov. m. r.*) carries a distinct blood-vessel which joins the right ovary in one of the neighbouring sections. The left ovarian mesentery (*ov. m. l.*) is cut near its dorsal end, where it forms a bridge passing from the body-wall to the median mesentery, and thus isolates a section of the third body-cavity. The external openings of the oviducts in *C. dodecalophus* are situated in epidermic recesses, as in *C. levinseni*.

In *C. gracilis* I do not find any epidermic recesses connected with the external apertures of the oviducts. These apertures are situated very close together (Pl. VI, fig. 61) on a part of the dorsal swelling of the metasome which is very prominent in some specimens (Pl. III, fig. 22). The pigmented oviduct extends completely up to the level of the epidermis (figs. 45—51) and opens on the convex surface of the dorsal swelling. The relations of the ovarian mesenteries are essentially the same as those of the other species, with the exception of the fact that the median dorsal mesentery of the body is incomplete in *C. gracilis*, and the ovarian mesenteries join the part of it which persists, namely that which is attached to the pharynx. The mesentery here carries a large and very conspicuous vascular space (figs. 45, 68) and it is easy to demonstrate that this gives off a conspicuous blood-vessel which runs in the ovarian mesentery to the dorsal part of the ovary. Evidence to this effect is not wanting in the other species, but I have seen it most conclusively in *C. gracilis*. One important function of the ovarian mesentery is thus to carry the nutritive blood-vessel of the organ. That vessel having found its way to the ovary there is no further use for the mesentery, which accordingly disappears in the ventral part of the ovary.

It is not easy to account for the universal occurrence of the pigment of the oviducts. I have, in Section VII (p. 27), called attention to the suggestion of M'Intosh that this substance may have something to do with phosphorescence; and I have mentioned the resemblance which

appears to exist between the narrow pigment-line of the proboscis and the oviducts in the constitution of the pigment. It is not impossible that the pigment of the oviducts has an excretory function, with which its resistance to solution by spirit is quite in accordance. Fig. 46 (*C. gracilis*) gives some evidence that the pigment can be discharged to the exterior from the aperture of the oviduct; but it is quite possible, in the absence of further evidence, that this appearance is unnatural.

C. sibogae.

The most interesting outcome of my work on the "Siboga" material is the discovery of the males of *Cephalodiscus*. It is of course impossible to say how far the facts observed in *C. sibogae* will be found to apply to other species; but in view of the very small amount of anatomical differences, in other respects, between species which are at first sight extremely unlike one another, I suspect that what is true of *C. sibogae* will be found, with modifications, to be of general application in the genus.

The ordinary zooids of *C. sibogae* are usually completely sterile or neuter individuals (Pl. I, fig. 3), though in immature blastozooids (Pl. XIII, fig. 184) the reproductive organs may be represented by a pair of minute vestiges (*g.*), similar in position to the ovaries of the other species. I am inclined to regard the neuters as modified males rather than as modified females, since I have found at least one case in which functional testes appear to be present in a specimen which otherwise resembles a neuter.

In the tangled masses of zooids which occur in the basal jelly of the colony are found considerable numbers of individuals of an entirely different appearance (Pl. VII, figs. 72—76); and these are the males. While shewing the general *Cephalodiscus* structure in an unmistakeable way, the males have very remarkable peculiarities of their own, the most striking of which is the complete want of any arrangements for taking food. This is indicated by the absence of tentacles and of the operculum, and by the vestigial character of the alimentary canal.

A full-grown male, drawn to the same scale as the neuter individual, fig. 3, is represented in fig. 75, from which it will be seen that there is not much difference in size between the males and the neuters. This individual was cut into frontal sections, some of which are shewn in figs. 80—89 (Pl. VIII). The proboscis (*p.*) is rather small, but it has the same relations as in normal *Cephalodiscus* zooids, and even possesses the characteristic line of red pigment across its ventral lobe. The collar is produced into a single pair of arms (*R. a.* and *L. a.*), which possess no trace of tentacles. The epidermis of these curious arms of the male is, except for a short region at the base, almost entirely constituted by enormous numbers of refringent vesicles (Pl. IX, fig. 99), similar to those which occur in the terminal knobs of the arms of the female *C. dodecalophus* or in those of some of the arms of *C. gracilis*. The arms seem to be subject to great variation in length. In the individual shewn in fig. 75 they are relatively short, but in other cases they may be at least twice as long. The refringent vesicles make their appearance at a young stage, and there is some evidence that they may become used up in some of the older males. In other cases, however, they are still present in undiminished numbers in individuals in which the testes are fully developed.

The single pair of arms of the male *C. sibogae* agree in position with the first pair of arms of an ordinary *Cephalodiscus*; or, in other words, they are developed from the anterior end of the dorsal side of the collar (figs. 72, 74).

The metasome is much the largest part of the adult male, and it is almost entirely filled by a pair of large testes, one of which is usually longer than the other. The body passes gradually into a long, slender stalk, although I have not been successful in obtaining specimens in which this is complete. It will be noticed that the stalk is attached to the extreme end of the body, and does not originate from its anterior side as in the female zooids of other species.

The young male (fig. 72) differs from an ordinary *Cephalodiscus* bud in no striking character except that of the arms. The proboscis is of great size, as is usual in buds, and its buccal disc overhangs the whole of the collar and metasome. The dorsal part of the collar (*c. n. s.*) is indicated by an obvious swelling, separated from the body by a constriction. From the anterior region of this swelling originate the two characteristic arms, with their epidermis crowded with refringent vesicles (not shewn in the figure). The left arm has been broken off in this individual, but its torn base (*L. a.*) is clearly visible. The metasome is constituted by the slightly swollen portion which immediately succeeds the collar, and it passes without any line of demarcation into the stalk.

Other young males, which differ in no essential respect from the above, are shewn in figs. 73, 74. In some cases, indications of the alimentary canal, the collar-pores and the gonads can be seen through the body-wall. In fig. 73 the right testis (*t. r.*) has reached a moderate size, while the left testis, partially concealed by the right arm, is smaller. The left arm of this individual is bifurcated at the tip.

It will be noticed that the principal difference between the young and the adult male is in the proportions of the metasome, which increases, concurrently with the development of the testes, to a large size, the other regions remaining stationary in their growth.

A second adult male, in which the body-wall has been accidentally torn, is shewn in Pl. VII, fig. 76 and Pl. IX, figs. 95, 96. The testes are elongated bodies which, as in several other cases observed, shew constrictions or lobulations at intervals. The posterior end of the left testis (*t. l.*) has been broken. The ventral lobe of the proboscis is turned dorsally, the pigment-line being thus seen through its posterior epidermis. This position is favourable for the examination of the mouth (fig. 95, *m.*), a more or less triangular aperture which appears to lead into the vestigial alimentary canal indicated in the figures. Close to the anterior wall of the pharyngeal portion of the alimentary canal are a pair of collar-canals (*c. c.*). I have not found gill-slits in any of the males, and in view of the absence of the tentacles, it is hardly to be expected that they are present; but the material is not sufficiently well preserved to enable me to be certain of their absence. The rectal limb of the alimentary canal is indicated in figs. 95, 96 by a slender cylindrical mass of cells (*r.*) which is seen near the left testis.

The posterior view of the same individual (fig. 96) shews the distinct collar-swelling indicating the position of the central nervous system (*c. n. s.*). Immediately posterior to this, the metasome rises into a dorsal swelling, as in an ordinary female zooid; and on the anterior part of this swelling, close behind the end of the collar, I believe that I have been able to

make out the two generative pores (*g. p.*). Posteriorly to the inner edge of the left testis is seen the vestigial rectum (*r.*), and between this and the central nervous system is a conspicuous blood-space (*d.v.*). The strand connecting this blood-space with the rectum may be a contracted part of the vessel.

Fig. 79 is a more or less sagittal section of an old male, in which however the proximal end of the body was bent round in such a way as to be cut transversely, thus exposing both the testes. Although the state of preservation is not all that could be desired, there can be no doubt of the existence of the three body-cavities characteristic of *Cephalodiscus*, of a central nervous system, and of a collar canal.

Figs. 80—89 are sections nearly transverse to the long axis of the old male shewn in fig. 75. Fig. 80, through the proboscis and the two arms, indicates that each of the latter has a distinct central cavity. This cavity, which is continuous with that of the collar, is limited by a definite basement-membrane, which in some of the imperfectly preserved male individuals is exposed by the loss, by maceration, of the vesicle-containing epidermis. The membrane probably has a supporting function, as in the arms of a normal zooid. The epidermic vesicles, in this specimen, have a degenerated appearance, and are not well stained. The cavity of the left arm (*L. a.*) shews distinct evidence of lodgitudinal muscles at the distal end, where it is cut tangentially, and of fibres passing transversely across the cavity in the rest of its extent.

Fig. 81, through the anterior part of the central nervous system (*c.n.s.*), shews the cavity of the left arm opening into the dorsal horn of the collar-cavity, here lined by a very definite epithelium; a similar space occurring on the right side of the section. The space between the two dorsal horns, and underlying the central nervous system, is the pericardium; it contains a considerable number of nuclei, the exact arrangement of which is uncertain. The next (more dorsal) section shews some indication of the external part of the left proboscis-pore, though not with sufficient clearness to justify me in asserting that proboscis-pores exist in the male.

In the next section more ventrally (fig. 82) the pericardium no longer appears, and the two collar-cavities are separated by a dorsal mesentery, at the ventral end of which an excessively minute notochord is indicated.

In fig. 83 the notochord is still visible, the right arm opens into the collar-cavity, and the pigment-band of the proboscis has come into view. The proboscis is extremely muscular, the muscles on the left side of its cavity being cut transversely.

Fig. 84 cuts the mouth (*m.*) and the left collar-canal (*c. c.*), behind which are the lateral nerve and the left testis (*t.*).

Fig. 85 shews the right collar-canal, with the corresponding lateral nerve, and the pharynx (*ph.*) supported by a dorsal mesentery which carries a minute blood-space. This mesentery gives off a branch to the left testis, while on the right side is seen the corresponding generative pore (*g. p.*).

Three sections further (fig. 86) the alimentary canal has become very small. Both testes are now seen, with the conspicuous dorsal vessel (*d. v.*), containing a coagulum and giving off vessels to the testes. These travel along paths which may be regarded as lateral mesenteries, similar to the lateral or ovarian mesenteries found in the female *Cephalodiscus*.

In fig. 87, the alimentary canal is represented by an excessively small structure, in which a lumen can barely be detected. As this immediately precedes the appearance of the recurrent or rectal limb of the canal, it appears to correspond with the stomach or the second stomach of the female. The vestigial character of the alimentary canal is thus distinctly indicated, and it can hardly be rash to assert that no digestion takes place in the male zooid. The dorsal vessel has reached its maximum size in this section, and the vessels to the testis are distinct. The ventral mesentery is probably complete on the side of the alimentary canal opposite the dorsal vessel.

Two sections later (fig. 88) the recurrent limb of the alimentary canal is seen as a cylindrical body with an obvious lumen. This meets the body-wall at one point, which probably represents the anus, although I have not observed any indication of an actual perforation. The rectal limb of the alimentary canal was obviously lying in a nearly frontal plane; and it will be noticed that in the individual shewn in figs. 95, 96, the rectum travels but a short distance in the direction of the anterior end of the animal. The dorsal vessel in fig. 88 is continued as a lobe which lies to the left of the rectum, the right testicular vessel being also visible. In the next section the dorsal vessel has completely disappeared, without apparently giving off any branch in this direction.

The proximal part of the male is of fairly uniform structure (fig. 89). The body-cavity remains spacious, and there are distinct indications of a median mesentery. At the two extremities of this mesentery are an anterior and a posterior vessel (*a. v.*, *p. v.*) which, in the particular male figured were more distinct near the stalk than nearer the other end of the metasome. The anterior side of the body-wall has a layer of longitudinal muscles (*ms.*) which correspond with those of an ordinary female *Cephalodiscus*.

There can be no reasonable doubt that the two vessels shewn in fig. 89 are continued into the two stalk-vessels which I believe to be typical of *Cephalodiscus*. It will be noticed that the relations of these vessels in the greater part of the testicular region of the animal is like those of the vessels in the stalk of an ordinary zooid; that is to say, each vessel is closely apposed to the inner side of the body-wall. The anterior vessel is indeed found in this position in the body of the female zooid, but it will be remembered that the posterior vessel, on entering the body, in the female, becomes attached to the second stomach (fig. 22). Taking these facts into account, and considering further the position of the bend of the alimentary canal, it appears that the greater part of the "body" of the male is really a dilated part of the stalk; or in other words that the testes have grown far beyond the limits of the body, as that term is understood in the female, and have extended into the cavity of the stalk.

This fact may have some bearing on the remarkable statements made by Conte and Vaney (**02**, 1, p. 64) with regard to the testis of *Rhabdopleura*. That organ was described by Lankester (**84**, p. 633, Pl. XL, fig. 7) as an asymmetrical body, situated on the right side, and opening near the anus. It has in fact much the same position as one of the gonads of a female *Cephalodiscus*, except that in some cases it appears to form a hernia-like projection of the body-wall in which its blind end lies. Lankester points out that the young testis is possibly represented by the "cellular body" described by Sars (**72**, p. 5, Pl. II, fig. 15, *r*) in the same animal.

LANKESTER's account is confirmed by CONTE and VANEY, but the testis is said to be "une différentiation de l'extrémité antérieure du pédoncule", the axial part of which gives rise to the testis. It is not quite clear what is the precise meaning of this passage, taken in conjunction with the statement that LANKESTER's account is correct; nor do I profess to understand the short description given by the same observers of the ovary of *Rhabdopleura*. But what is said of the testis may perhaps indicate that this organ is developed at the anterior end of the metasome (as in *C. sibogae*) before that part shews any differentiation into body and stalk.

It is hardly necessary for me to criticize CONTE and VANEY's account of the general morphology of *Rhabdopleura*, and I may merely refer to the remarks made by FOWLER (**04**) on the subject. But I think there can be no reasonable doubt that *Rhabdopleura* is really related to *Cephalodiscus*, and the denial by CONTE and VANEY of the presence in *Rhabdopleura* of such organs as the collar-pores or of subdivisions of the body-cavity are directly controverted by the careful work of FOWLER (**92**, 1, 2; **04**) and SCHEPOTIEFF (**04**), as well as by the few observations I have been able to make on the same subject.

In the case of the zooid of *C. sibogae* shewn in fig. 3, there is some evidence of the existence of a single, posteriorly situated testis [1] similar to the organ described by LANKESTER in *Rhabdopleura*; while in the specimen to which the abnormal arm shewn in fig. 98 belongs there appear to be two testes situated in the third body-cavity, in the position of the ovaries of a female *Cephalodiscus*. I do not feel quite confident of the accuracy of these observations, but it does not seem to me impossible that one of the individuals which is normally neuter may exceptionally develop a testis. If this is really the case, it appears to imply that the vestigial gonads of the neuter are to be regarded as testes, and the neuters themselves as males with suppressed gonads. But this conclusion rests on too slight a basis to be worth much. I need hardly say that I have no evidence that anything like protogynous hermaphroditism occurs in *Cephalodiscus*, as is believed by CONTE and VANEY to be the case in *Rhabdopleura*.

Two questions relating to the physiology of the male will at once occur to any one conversant with the facts; — namely (I) the mode of nutrition, and (II) the function of the curious vesicles of the epidermis of the arms.

(I) Nutrition of the male.

It has just been shewn that the alimentary canal of the male is a vestigial structure. There is no trace of a glandular stomach; and moreover the arms are not provided with tentacles, and there is no recognisable operculum. Vestiges of food-grooves can, however, be distinguished in section at the bases of the arms, which in other parts are circular in section.

The male has on the contrary a well developed vascular system; and it appears to me that this is the direction in which one must look for the solution of the question indicated. The males are probably nourished by the neuter individuals, through the medium of the vascular system, in a manner analogous to that in which the nutriment absorbed by one set of individuals in *Doliolum* is said to be transferred through the vascular system of the asexual form to an entirely different set of individuals.

1) This is not shewn in the figure, which represents an anterior view.

I have unfortunately been unable to trace the stalks of the males into continuity with those of the neuters. But it is a striking feature of this species that there occur, here and there in the colony, discoidal masses of tissue from which originate a number of stalks (Pl. VIII, fig. 94). Somewhat similar masses occur in *C. gracilis*, in which it is not difficult to ascertain that the mass in which a number of stalks unite represents the budding region of an old stalk, as may be seen by referring to the group of buds shewn in Pl. I, fig. 4.

It may thus be inferred, with a reasonable degree of probability, that the union of a number of stalks in a common disc (fig. 94) implies that all the individuals represented by these stalks are the blastozooids produced by a single budding individual. I am not in a position to shew that some of these stalks belong to males and others to neuters, but I regard it as in the highest degree probable that this is the case, and that the nutrition of the male takes place by means of the union of its vessels with those of a neuter individual (or individuals) though the common stalk-base.

The state of preservation of the material is not suitable for the detailed examination of the vessels of the stalk; but I have convinced myself of the existence of both anterior and posterior stalk-vessels, as in other species of *Cephalodiscus*. There is also evidence that a vascular continuity between the stalks of different individuals does exist in the stalk-bases. In one case it appeared that the posterior vessel of a stalk passes into the interior of the stalk-base, and travels, in the middle of the cavity of that structure, far enough to underlie the base of the next stalk. The appearances suggest the exist of a vascular plexus in this position, and there is some evidence that the vessels of other stalks communicate with this plexus. The anterior vessel of the stalk first alluded to can be traced as far as the basement-membrane of the basal ectoderm of the common disc, although its exact mode of termination is uncertain.

The principal difficulty in this view of the nutrition of the male zooids is the large size of the dorsal vessel (Pl. VIII, figs. 86, 87). It has been argued above that this vessel, in the female *Cephalodiscus*, is a nutritive structure which conveys the products of digestion to the ovaries. The vessel in question is certainly not less developed in the male than in the female, and yet it starts from a stomach-region which is so vestigial that no stomach can be discriminated from the rest of the alimentary canal. A further difficulty is that I have been unable to discover any vessels from which the dorsal vessel could derive its blood.

It is not inconceivable that the alimentary canal, though vestigial as a digestive organ, might be capable of taking in some nutritive secretion discharged by the neuter individuals into the cavities of the coenoecium. The mouth of the male is sufficiently well developed to make this possible. But any hypothesis of this kind could hardly be accepted without more definite evidence in its favour; and it seems more reasonable to look elsewhere for an explanation of the large size of the dorsal vessel.

The explanation which appears to me most probable is that this receives its blood from the posterior vessel of the stalk and of the proximal part of the body, and that its large size adapts it for acting as a reservoir of blood. I have not been able to demonstrate any continuity between the two vessels in question; and indeed the posterior stalk-vessel in passing forwards

becomes more and more obscure, and cannot certainly be recognised in the region of the intestinal loop of the gut. I do not think that this forbids the assumption I have just indicated. The thin-walled vessels of *Cephalodiscus* are very difficult to distinguish in their empty condition, and the failure to find a vessel in a particular case is no proof that it does not exist. It will be remembered that, in the female *Cephalodiscus*, the posterior stalk-vessel ends in the wall of the second stomach, and I have suggested above that its blood, after passing through the sinuses of the alimentary canal, finally makes its way to the dorsal vessel. With the practical disappearance, in the male, of the first and second stomachs, the posterior stalk-vessel might still retain its function of supplying the dorsal vessel. On *a priori* grounds therefore it appears to me probable that there is an indirect communication between these two vessels.

(II) The function of the epidermic vesicles of the arms of the male.

I think there can be little doubt that these structures are homologous with the vesicles which occur in the end-bulbs of the arms of the females of certain species, and especially of *C. dodecalophus*. I have not found them in *C. levinseni*, but they are well developed in the anterior pairs of arms in the buds of *C. gracilis*, and sometimes at least they persist in the adults of that species.

I have in one or two cases noticed appearances (Pl. IX, fig. 98) for which I cannot quite account, in *C. sibogae*. An ordinary tentacle-bearing arm has been found, in a partially teased preparation, with its distal end prolonged into an elongated, vesicle-bearing portion without tentacles, similar to the entire arm of a male. I think there is little doubt that this is a correct observation, though in view of the tangled condition of the zooids the possibility is not quite excluded that the arm of a male has adhered to that of a neuter by defective preservation. There is, however, practically no doubt that the arm shewn in fig. 98 is in continuity with an individual which bears tentaculiferous arms and has the general characters of a neuter. But it also appears that the metasome of this individual contains, in the position occupied by the ovaries of an ordinary *Cephalodiscus*, a pair of small testes, which seem to be functional organs. I therefore regard this case as one of correlated variation, in which a zooid has not only the male character of possessing testes but also the associated character of developing numerous vesicles on one of its arms. I cannot, unfortunately, decide whether the abnormal arm belongs to the first pair, though this is by no means impossible. It must further be pointed out that there is some difficulty in disentangling a complete zooid from the mass of somewhat badly preserved individuals found in the basal encrustation of the coenoecium; and it is thus not impossible that all the neuters may have one or more of their arms prolonged into vesicle-bearing portions. The evidence is, however, distinctly opposed to any such view; and fig. 98 thus appears to represent an abnormality.

If the vesicles of the male arms represent those of the end-bulbs of the arms of *C. dodecalophus*, it is probable that their function cannot be one which is exclusively correlated with the other peculiarities of the male. This makes it less probable that the vesicles have the nature of reserve-supplies of nutritive material, developed precociously in the young bud for the nutrition of the future testes. Some support might be given to this view by the fact that some

of the old males seem to have lost most of their vesicles; although, on the other hand, others shew no trace of this tendency.

MASTERMAN (**97**, 2, p. 344) suggested that the end-bulbs of *C. dodecalophus* had the nature of compound eyes, a function which their position makes not improbable; although he subsequently abandoned that hypothesis (**03**, p. 725). COLE (**99**) on the other hand believes that the vesicles are comparable with the rhabdites of Turbellaria. Although I have not examined the structures with the aid of the histological methods recommended by COLE, the suggestion of this observer seems to me not improbable. If this were the case it would follow that the male individuals of *C. sibogae* are not only the individuals which produce the spermatozoa, but that they have a subsidiary function, analogous to that of the dactylozooids of Hydrozoa, of producing weapons for the defence of the colony. It may be presumed that the zooids of both kinds can be protruded more or less from the orifices of the coenoecium. It is not difficult to imagine that the long arms of the immature and adult males, waving about in the water among the plumes of the neuter zooids, might be valuable weapons of defence, on the assumption that COLE's view that the end-bulbs of *C. dodecalophus* are rhabdite-batteries is the correct one.

It seems to me not impossible that the remarkable "Härchen" of the epidermis of *Phoronis gracilis*, of which a description has recently been given by DE SELYS LONGCHAMPS (**03**, p. 28, figs. 22—26), may be comparable with the epidermic vesicles of *Cephalodiscus*.

XVI. BUDDING.

The details of this process have been described by MASTERMAN (**98**, 2), some of whose more important results may be summarised as follows. —

The buds are formed on either side of the middle line of the parent stalk, from the proximal, sucker-like extremity of that structure. A new bud may develop from the stalk of a young individual which has not yet become free. The tissues of the bud are derived entirely from ectoderm and mesoderm, the endoderm taking no part in the process. The coelomic cavities are formed from that of the parent stalk, and in the youngest stage observed are represented by a single pair of cavities, completely subdivided by a median mesentery, and continuous with the cavity of the stalk of the adult. The mesentery contains a vessel which is given off by the anterior stalk-vessel. The vessel contained in the bud assumes a dorsal position distally, where it dilates to form the "subneural sinus". The proboscis early becomes conspicuous, its undivided body-cavity being the distal extremity of the coelom of the young bud, although it is not explained exactly how the unpaired anterior body-cavity is related to the paired coelom of the more proximal part of the bud. It must be supposed from the account given, and particularly from a consideration of MASTERMAN's figures 29 and 30 that the median mesentery ends abruptly before reaching the distal end, which is accordingly undivided. The alimentary canal early makes its appearance as an ectodermic invagination, the orifice of which persists as the mouth. At about the stage when the first pair of arms begins to be indicated externally, the enteric sac

meets the body-wall at two circular lines of contact, thus dividing the coelom into the unpaired proboscis-cavity and the two pairs of cavities characteristic of the adult. The external division of the bud into the three regions has meanwhile been progressing. The future metasome is directly continuous with the young stalk, and its body-cavities are hence prolongations of those of the parent stalk. The intestinal limb of the alimentary canal develops as a dorsal diverticulum of the originally simple enteric sac, and fig. 39 of the original memoir shews it passing from its origin freely through the body-cavity, the coelomic epithelium dipping down between it and the stomach. The intestine grows dorsally till it meets the body-wall, when it opens to the exterior by the anus, which is from the first in its definitive position. The pharyngeal region gives rise to evaginations which form the notochord and the gill-slits. The ovaries are developed from the wall of the coelom; but the oviducts, like the collar-pores, are ectodermic invaginations. The arms are of course formed as dorsal outgrowths of the collar.

Fowler (**04**), in describing the budding of *Rhabdopleura*, states that most of the alimentary canal is probably derived from a thin-walled tube present in the mesentery of the parent-stalk, and he supposes that this tube is of endodermic origin. The commencement of the alimentary canal is, however, believed to be formed from ectoderm, and it is from this stomodaeal portion that he believes the notochord to originate.

The analogy of the Tunicata shews that there is no *a priori* improbability in Fowler's account of the origin of the alimentary canal; and the supposed endodermic tube of the stalk could be regarded as an epicardium-like formation. From such observations as I have been able to make on the budding, I am, however, inclined to think that Masterman is right in deriving the entire alimentary canal of the bud from ectoderm, a process which is believed by the majority of investigators to take place in the budding of the Ectoproct Polyzoa. I have, moreover, given reasons above (p. 78) for believing that the "endodermic" tube in the stalk of *Rhabdopleura* is the posterior stalk-vessel. Fowler has not, as a matter of fact, brought forward evidence shewing that this structure gives rise to any part of the alimentary canal of the bud; and, on the analogy of *Cephalodiscus*, I consider it probable that the entire alimentary canal of *Rhabdopleura* is derived from a single "Anlage". If this be the case, Fowler's contention that the notochord of *Rhabdopleura* is morphologically ectodermic loses most of its force, since it might be argued on similar grounds that the entire alimentary canal of *Cephalodiscus* is to be regarded as a stomodaeum.

It may be noted that Masterman's account of the origin of the coelomic cavities of the bud is similar to that which has been given by Schultz (**03**, 1) of the origin of the cavities in regenerating specimens of *Phoronis*, in which both the preseptal and the postseptal cavities are derived from the general body-cavity.

There appears to be a marked contrast between *C. dodecalophus* and *C. levinseni* on the one hand, and *C. gracilis* and *C. sibogae* on the other hand, in respect of the extent to which the blastozooids remain connected with one another. It may, however, be remarked of *C. levinseni* that the colony appears to have been killed at a season when budding was not taking place with special activity.

C. gracilis and *C. sibogae* on the contrary shew a distinct tendency to the production

of small colonies of individuals, connected by the basal disc from which the whole series of buds has been developed. A characteristic group of young individuals of *C. gracilis* is represented in fig. 4, but the mass in this case consists of the products of two budding individuals, which are represented respectively by the letters *A* and *B*. *A*. 1—4 are deeply pigmented bodies, probably representing degenerated stalks, *A*. 1 being the main stalk. The bodies of the zooids had presumably been lost before or at the commencement of the degeneration of the stalks. The only healthy zooid belonging to this group is the young bud *A*. 5. The second group (*B*) consists of a budding disc prolonged into the structure *B*. 1, which is clearly the base of an old stalk whose zooid has degenerated. *B*. 2 is a pigmented body, probably a stalk whose degeneration took place some considerable time before the specimen was killed. *B*. 3 has also lost its zooid, but its degeneration has not advanced far. *B*. 4 is a healthy bud which is seen from behind. The limit between its collar and its metasome is distinct, while the collar is produced into five arms on the right side and three on the left. The first arms of both sides already bear tentacles, and each ends in a swollen knob filled with refringent vesicles, as in *C. dodecalophus*. The base of the third right arm of this bud is concealed by the second and fourth arms, beneath which the distal part of the arm can be detected. *B*. 5 is a somewhat younger bud, seen from in front. *B*. 6 is still younger, and is seen from the side. The collar and the metasome are already clearly marked off from one another, and a single pair of arms, represented by their vesicle-bearing knobs, are developed, although they are not well shewn in the figure. *B*. 7 is a very young bud, in which the proboscis is already marked off from the more proximal part. All these structures, *B*. 2—*B*. 7, are derivatives of the disc (*d*.) which constitutes the base of *B*. 1.

Groups of this kind occur in considerable numbers throughout the coenoecium. In at least one case evidence was obtained tending to shew that degeneration of a zooid begins by the throwing off of the proboscis and collar, leaving the metasome, with the alimentary canal, attached to the stalk. The number of structures which can be interpreted in no other way than as the basal ends of degenerated stalks seems to shew (I) that degeneration of the zooids is of frequent occurrence, and (II) that it is usually not succeeded by any regeneration of the lost parts.

One of the youngest buds observed is shewn at the base of the stalk in Pl. I, fig. 7 (*C. gracilis*) and more highly magnified in Pl. III, fig. 26. The distal end of the bud is swollen into an ovoid form and is easily recognisable as the future proboscis. The anterior body-cavity, lined by a distinct epithelium, can clearly be seen in optical section. The swollen region which intervenes between the proboscis and the base of the old stalk probably represents the collar + metasome.

Fig. 27 is a rather older bud of the same species, somewhat less magnified than fig. 26, and is attached to the basal disc of a zooid which has not degenerated. The proboscis has assumed its adult character, being already flattened in an antero-posterior direction, and it is convex anteriorly and concave posteriorly. The collar, which could not be distinguished from the metasome in the earlier stage, is now well marked, and is growing out dorsally into the first pair of arms. Both proboscis and collar have well marked cavities, but it cannot definitely be ascertained whether these cavities are continuous with one another or not.

Fig. 8 is a posterior view of an older bud, considerably less magnified, and corresponding

in the degree of its development with *B.* 6 in fig. 4. The proboscis has acquired its pigment-line, while the two arms of the first pair are short bodies, each ending in a knob containing refringent vesicles. The collar is marked off dorsally from the metasome by a slight groove. It may be noted that the male individuals of *C. sibogae* remain at this stage of development in respect of their arms and of the absence of any demarcation between body and stalk.

Fig. 30 is an anterior view of an older bud, more highly magnified. The proboscis is somewhat torn on the right side of the figure, and the first arm of the same side has been lost. The other first arm is a good deal longer than in fig. 8, and a second pair, also with vesicles, has been developed behind it. The mouth and a small alimentary canal are seen through the more or less transparent wall of the proboscis, while it may specially be noted that the lower lip or operculum (*op.*) is continuous with the second arms, which are for the moment those which are most posteriorly situated. Ovaries are already present, but are not represented in the figure.

Fig. 9 is a similar view of a somewhat older bud, in which some indication of the development of new arms may be observed. In fig. 32 four pairs of arms are present, five of which shew young tentacles. No vesicles can be found at the tip of the first arm of the left side, but a few are present in the corresponding right arm and in the second and third left arms. Their condition in the second left arm seems to shew that they are in process of being lost. This is probably a normal feature in this species, since it is practically certain that no vesicles are present in any of the arms of some of the adult individuals, although I have been able to recognise them at the tips of the first two pairs of arms in one or two adult zooids.

Most of the adult organs are already developed in fig. 32. The intestinal limb of the alimentary canal is seen in the foreground, while the mouth (*m.*) can be made out by deeper focussing. On the right side of this is seen the triangular lateral lobe of the operculum (*op. r.*). The two ovaries are visible, somewhat overlapped by the rectum. The body is still a direct prolongation of the stalk, and it may specially be noted that the arms are developed in such a position that their food-grooves at first face the posterior side of the proboscis. The posterior limb of the vascular loop of the stalk is seen attached to the bend of the alimentary canal.

Fig. 31 is a similar bud, seen obliquely from the left side. The alimentary canal has acquired its adult arrangement, and the left gill-slit (*g. s. e.*) and collar-pore (*c. c. e.*) are shewn in the figure, which further indicates the course of the food-grooves of the first three left arms on their way towards the mouth.

The bud *B.* 4 in fig. 4 possesses the full number (5) of arms on the right side, the fifth arm having the form of a nearly spherical swelling which is partly concealed by the base of the fourth arm. This specimen, like fig. 32, shews clearly that the arms are dorsal outgrowths of the collar-region.

Fig. 29 illustrates the fact that the stalk-vessels are well developed in the bud, a fact which is no doubt of great physiological importance in connexion with the supply of nutriment. The posterior limb of the vascular loop is, as usual, attached to the bend of the alimentary canal, while the anterior limb fades away in the anterior part of the body-wall of the metasome. Fig. 28 shews the two parts of the stalk-vessel of the same bud at a point a good deal nearer the base of the stalk.

I have been unable to obtain any confirmation of the account given by MASTERMAN of the changes in the position of the arms during the development of the bud. I have already discussed this question (p. 36), and I will merely repeat in this place that I believe that the complicated rotation of the arms described by that author does not occur, and that the hypothesis suggested to explain it is accordingly unnecessary.

In examining sections of buds of various ages, in *C. dodecalophus* and *C. gracilis*, I have come to certain conclusions which do not agree with those of MASTERMAN (cf. p. 91). There can be no question that the structure described by him as the "subneural sinus", in the later stages at least, is the pericardium. MASTERMAN has more recently (**99**, 2) admitted that the space which he at first described, in the adult, as the subneural sinus is in reality a pericardium, similar to that of Balanoglossus, although in his latest paper (**03**, p. 725) he states that it is evident that in his account of the budding "the origin of the pericardial sac must have been overlooked". From this I understand MASTERMAN to mean that while he would admit that the "subneural sinus" shewn in figs. 60 and 81 of his paper (**98**, 2) on the budding is the pericardium, he would probably maintain that the "subneural sinus" shewn in earlier stages such as figs. 36, 37 and 39 was really a vascular space. I am inclined to think, on the contrary, that the "subneural sinus" shewn by MASTERMAN in figs. 37 and 39 at least is the same structure as that of the later stages (figs. 80, 81). In all these cases the organ is represented as having no proper wall of its own, but as being a blastocoelic space between the ectoderm and the coelomic epithelium. This does not agree with my own results, and in further criticism of MASTERMAN's fig. 39 I must point out that I have reason to believe, from my study of the same species, that the proboscis-cavity is not really continuous with the paired body-cavities at a stage so late as this, nor does the intestine pass freely through the body-cavity from its point of origin in any of the young specimens which I have had under observation.

The buds of *C. dodecalophus* make their appearance, as pointed out by MASTERMAN, on either side of the middle line of the sucker-like base of the stalk, and on its anterior surface. Fig. 7, of *C. gracilis*, would at first sight seem to imply that the buds of this species are developed on the posterior side of the sucker. It must, however, be remembered that in the long-stalked species of *Cephalodiscus*, rotation of parts of the stalk round its own longitudinal axis are commonly observed, as may be seen by an examination of the course of the longitudinal muscles in entire preparations, or of the anterior nerve-tract in sections transverse to the long axis of the stalk. There is evidence of twisting in the stalk of fig. 7, and I think that the bud which faces posteriorly in the preserved specimen is really situated on the anterior side of the sucker. It is certainly a lateral bud, and a still younger bud is indicated by deeper focussing in the same specimen.

In its earliest recognisable condition (Pl. XIII, fig. 164, *b*.[1]) the bud of *C. dodecalophus* is a spherical vesicle lying in the thickness of the parent ectoderm, and formed as an outwardly directed bay of the basement-membrane. The interior of the parent-stalk is occupied by muscles and connective tissue which are developed to such an extent that no definite coelomic space remains, although the condition of the stalk throughout the development of the bud shews that the whole of the tissue internal to the basement-membrane of the epidermis must be regarded

as filling the third body-cavity of this region. The young bud is occupied by a derivative of this packing tissue; and although the cells in question may perhaps at first constitute a solid mass, they have arranged themselves as an epithelium surrounding a central cavity at the earliest stages recognised as young buds. The central cavity is in communication with the virtual cavity of the parent stalk; and although this communication is interrupted in the particular section figured (fig. 164), it is clearly seen in other sections of the same bud, and it is visible in the older bud (b^2) shewn in the same figure. The bud thus originates as a diverticulum of the third body-cavity, which shortly gives rise to a corresponding projection of the ectoderm. At its first appearance, as shewn in transverse sections, the diverticulum appears to be undivided.

At a slightly later stage (fig. 162), as stated by MASTERMAN (**98**, 2, p. 515), the cavity of the bud is divided by a prolongation of the anterior mesentery of the parent stalk. The parent mesentery carries a blood-vessel (*a.v.*), and although I have not been able to demonstrate the entry of a branch of this vessel into the bud I have little doubt that MASTERMAN is right in stating that this is the fact. I cannot, however, agree with him that the three divisions of the coelom remain continuous with one another up to the late stages shewn in his figs. 37 and 39. On the contrary, I find that in stages in which the ectoderm of the bud forms merely a hemispherical outgrowth of the parent stalk (figs. 161—163) a terminal coelomic vesicle ($b.c.^1$) is sharply marked off, and occupies the distal end of the bud.

Figs. 161—163 cut the parent stalk transversely to its long axis, and the bud is accordingly cut in a frontal direction. The three figures represent consecutive sections, fig. 161 being the one which passes nearest the base of the parent stalk. The lateral origin of the bud is clearly shewn by these figures. The proximal part is divided by a median mesentery, the right and left divisions of the coelom communicating freely with the parent stalk. The distal end of the bud in fig. 161 is occupied by a spherical vesicle, with a well marked coelomic epithelium. In the next section (fig. 162) the vesicle is divided from the paired coelom of the right side of the figure by a minute oval vesicle (*per.*?), which contains several nuclei. In the next section (fig. 163) the left paired cavity has almost disappeared, while the distal end of the bud is occupied by a cavity whose wall is not certainly constituted by an epithelium. I am unable to decide whether this cavity is continuous with the terminal cavity of fig. 162 or whether it is to be regarded as a vacuolated condition of the terminal ectoderm; but I am inclined to adopt the latter hypothesis. It is in any case quite clear that in the young bud of *C. gracilis* shewn in Pl. III, fig. 26, the end of the bud is occupied by a single ovoid epithelial vesicle.

Although I cannot identify the parts of the young bud shewn in figs. 161—163 with certainty, it appears to me highly probable, from a comparison with later stages, that the vesicle marked $b.c.^1$ is really the coelomic sac of the anterior body-cavity, that the paired cavities represent the third body-cavities and probably the collar-cavities as well, and that the minute structure *per.*? is the pericardium. There is no clear evidence to shew how these structures have originated [1]), though I consider it probable that they have been formed by the division of the single coelomic sac seen in the younger bud in fig. 164. It is not impossible that the

1) In regenerating specimens of Balanoglossus, DAWYDOFF (02) finds that the pericardium is derived from the proboscis-cavity, and the latter from the perihaemal spaces; the amputation having been made through the collar.

pericardium and the anterior body-cavity are the members of an anterior pair of coelomic spaces, and that they have been segmented off respectively from the distal ends of the right and left cavities of the proximal part of the bud. The view that the pericardium is the fellow to the anterior body-cavity has been suggested for Balanoglossus by BOURNE (**89**, p. 66) and SPENGEL (**93**, pp. 682, 689) but it may be remarked that the strictly median position of the pericardium in the later stages of *Cephalodiscus* and the fact that both proboscis-pores open into the anterior body-cavity are not in favour of this view. Some of the later stages (*e. g.* figs. 177 and 179 + 180) might suggest that the pericardium represents an independent somite.

Whatever view is taken of figs. 161—163 there can be no reasonable doubt that they indicate a segmentation of the coelom beginning at a very early stage in the budding, and that MASTERMAN (**98**, 2, p. 516) is mistaken in supposing that the coelom remains undivided until after the alimentary canal has become obvious.

Figs. 175—177 represent a later bud, cut nearly sagittally, the parent stalk being however cut more or less transversely to its main axis. The coelomic cavities are now separated from one another, although the third body-cavities are continuous with those of the parent stalk. This is shewn in fig. 175, in which *b. c.*^{2} represents the collar-cavity of one side. It is so closely connected with *b. c.*^{3} as to suggest that the two cavities have been developed as the result of the interruption of a single cavity by the formation of a transverse septum. The anterior body-cavity (*b. c.*^{1}) appears separated from the collar-cavity by a considerable interval, but this is partly because the proboscis is cut somewhat tangentially. Two sections further in the series, the walls of the first and second cavities are continuous with one another, while in the nearly median section shewn in fig. 176, both sets of paired cavities have disappeared, the proboscis being occupied by the anterior coelomic sac (*b. c.*^{1}) in front, while at its base is a smaller vesicle (*per.*) which can be recognised with certainty as the pericardium. In fig. 177, on the other side of the middle line, four cavities are visible, the pericardium (*per.*) intervening between the anterior body-cavity (*b. c.*^{1}) and the collar-cavity (*b. c.*^{2}), and already shewing the ventral ingrowth of its wall which will give rise to the heart. The alimentary canal is distinguishable, in this bud, as a thick-walled sac opening by the mouth (fig. 176, *m.*), which is in its definitive position on the ventral side of the proboscis. It is uncertain whether the whole of the internal mass in this figure belongs to the alimentary canal, or whether the posterior portion of it may be part of the wall of the third body-cavity, cut tangentially. A small part of the lumen of the alimentary canal is cut in the neighbourhood of the mouth. As regards its external characters it may be noted that the proboscis is spherical, shewing hardly any trace of the flattening which is so characteristic of the adult. The boundaries of the collar are slightly indicated externally.

Fig. 164 is a sagittal section of the terminal sucker of an old stalk, on the anterior side of which are two buds. The younger of these (*b.*^{1}) has already been described. The older one (*b.*^{2}), situated nearer the sucker, shews the continuity of its third body-cavity with that of the parent, while the small ovoid vesicle (*b. c.*^{2}) is almost certainly one of the collar-cavities. In fig. 165, another section of the same bud, the anterior body-cavity (*b. c.*^{1}) and the third body-cavity (*b. c.*^{3}) are unmistakeable, while it is highly probable that the vesicle marked *per.* is the pericardium and the structure marked *b. c.*^{2} is the collar-cavity of the opposite side to that which is shewn in fig. 164.

I fully admit that the evidence afforded by the stages which have so far been described is anything but convincing with regard to certain points, but in the next stage figured (figs. 178—180) we are on surer ground. The sections are in much the same plane as the preceding ones, and are from a bud in which the first pair of arms is beginning to develop.

In fig. 178 are seen the proboscis and collar with their respective cavities, the collar-cavity being prolonged into the developing arm (*a. 1.*). A portion of the metasome (*met.*), with its body-cavity, is cut tangentially.

In fig. 179, the proboscis and collar are cut medianly. The proboscis has not only become somewhat flattened, but it shews another of its adult characters in having a ventral lobe composed of a fold of ectoderm, with basement-membrane between the two layers, but not containing a prolongation of the proboscis-cavity. The pericardium (*per.*) possesses a thickening on its posterior wall which indicates the wall of the future vascular space. The mouth (*m.*) and part of the alimentary canal are well developed, although the posterior outline of the latter is obscurely marked off from the epithelium of the third body-cavity. The notochord (*nch.*) is present, beyond doubt, as a small diverticulum of the pharynx, reaching the wall of the pericardium.

In fig. 180, the middle line has been passed, so that the other collar-cavity and first arm are cut, while the coelomic sac of the proboscis is cut tangentially. The bud was probably not lying with its axis in one plane, since the trunk is cut obliquely transversely to its main axis. The intestinal limb of the alimentary canal, which meets the body-wall in the position of the future anus, is connected with the ventral wall of the body by the median mesentery, on either side of which are the paired third body-cavities.

Assuming that the pericardium here described is MASTERMAN's "subneural sinus", it will be noticed that this specimen lends no support to the statement of that author (**98**, 2, p. 516, figs. 37, 39) that the notochord (= "subneural gland") is at first at some distance from the pericardium (= "subneural sinus") and at a later stage shifts its position so as to meet it.

I think that there is very little reason to believe that the structure marked *sn. g.* by MASTERMAN in fig. 37 has anything to do with the "subneural gland", a structure which I describe under the name of notochord. In stages so late as his figs. 37 and 39 I should not have expected to see a body-cavity extending continuously from the proboscis to the metasome on the ventral side of the pericardium; and for this reason and for others which I have explained above I cannot consider the figures in question as anything but diagrams (probably combination-figures), representing MASTERMAN's views with regard to the structure of the buds.

The five body-cavities and the pericardium are easily recognisable from the stage represented in figs. 178—180 onwards, the third body-cavities remaining continuous with those of the parent-stalk until the bud is liberated, except so far as they are obliterated in the stalk of the bud by the development of muscles and connective tissue. The early appearance of the pericardium as a sharply marked epithelial sac is certainly one of the most characteristic features of the budding of *C. dodecalophus*.

The bilateral origin of the buds is well shewn in figs. 169 and 172.

The parent stalk is turned forwards towards the proboscis, and its terminal sucker is cut

nearly frontally. Fig. 172 cuts the free end of the stalk tangentially, so as to shew a thick mass of ectoderm (*d.*) which is the edge of the sucker. In this mass are seen the third body-cavities of two buds (*b.*[1], *b.*[2]) of different ages, in each case subdivided by a median mesentery. The middle line of the actual anterior edge of the sucker corresponds with the interval between the two buds, as is seen in sections which cut the parent stalk nearer its central axis. Some of these sections demonstrate the continuity between the cavities of the buds seen in fig. 172 and that of the old stalk.

Fig. 169 shews the highly crumpled condition of the ectoderm and of the basement-membrane, due to the contraction of the muscles of the stalk. Part of the edge of the sucker is still seen as two masses of ectoderm in contact with the younger bud (*b.*[1]). In both the buds, the edge of the mesentery which is further from the parent stalk corresponds with the anterior surface of the bud. The older bud (*b.*[2]) is cut somewhat obliquely through its stalk, the part which is nearer its base being still indicated by the third body-cavities.

The structure of the younger bud, which is cut in a direction at right angles to its long axis, may be studied from before backwards. Fig. 166 shews two cavities, lined by a distinct epithelium, of which the smaller, the pericardium (*per.*), is more dorsally placed. The larger (*b. c.*[1]) is of course the anterior body-cavity. The pericardium is absolutely median, so far as can be seen, although it has not been found possible to decide whether it is a median structure or not in the younger stages. A section corresponding with fig. 166, though somewhat older, is figured by M'Intosh (**87**, p. 28, Pl. V, fig. 3), although the pericardium, which is marked *vc.*, is supposed to be part of the collar-cavity.

Fig. 167 cuts the bud at the level of the collar-cavities and of the mouth (*m.*) which is overhung by the ventral lobe of the proboscis. In the next section, the alimentary canal appears as a single vesicle, while in the next (fig. 168) the centrally placed nuclei (*al.*) belong to the enteric sac, while the cavities at the sides (*b. c.*[3]) are the third body-cavities. While the inner limit of the epithelium of these cavities is very distinct, the outer outline is much less so, and I have not been able to identify with certainty the boundary between the antero-ventral ectoderm and the internal tissues of the bud. Some of the thick ventral wall (upper in figures), both of this section and of the section of the same bud (*b.*[1]) shewn in fig. 169 may really belong to the coelomic wall, and there are appearances in the sections which suggest that a proliferation of cells takes place on the outer side of the coelomic epithelium, in the anterior and antero-lateral regions, to give rise to the musculature of the body and stalk. The alimentary canal has disappeared in fig. 169, although the median mesentery persists as far as the junction with the parent stalk, both in this and in the older bud (figs. 169, 172). The mesentery seen in fig. 169 (younger bud) appears to contain a blood-vessel, while as another indication of a probable vascular space may be noticed the interval shewn in figs. 167, 168 between the epithelium of the alimentary canal and the coelomic epithelium.

Fig. 170 is a section transverse to the principal axis of the older bud shewn in fig. 169. The alimentary canal is in contact with the posterior body-wall, and the intestine (*int.*) is being constricted off from the stomach (*stom.*). In the section (fig. 171) of the same bud next in front of fig. 170 the intestine has been completely constricted off, and it fills up the interval between

the stomach and the posterior epidermis; the two divisions of the alimentary canal lying in a common peritoneal investment, formed exactly as in fig. 170. The same section shews one of the ovaries (*ov.*) as a minute body continuous with the coelomic epithelium, from which it has probably been developed, in accordance with MASTERMAN's statement (**98**, 2, p. 519) to that effect.

Figs. 173, 174 are drawn to shew the great proportionate size of the notochord (*nch.*) in the bud, a fact already commented on by M'INTOSH (**87**, p. 28), and the obliquity of the first and second body-cavities to the long axis of the bud. The proboscis with its body-cavity, and the pericardium have already acquired their adult relations. This bud still possesses a single pair of arms.

My observations on the first development of the alimentary canal in the bud are, so far as they go, in favour of MASTERMAN's view (**98**, 2, p. 515) that the entire alimentary canal develops as an ectodermic invagination; and they are consequently opposed to those of FOWLER (on *Rhabdopleura*), according to which part of it is a derivative of an endodermic tube in the stalk. From the earliest stage in which I can recognise the alimentary canal, this organ appears to open definitely to the exterior by the mouth, and I have noticed no discontinuity of the kind which would be implied by FOWLER's view that while most of the canal is endodermic, the anterior part is developed as a stomodaeum.

With regard to the later development of the alimentary canal I cannot, however, agree with MASTERMAN, according to whom the intestinal limb of the alimentary canal is developed as a diverticulum from the ventral and posterior end of the enteric sac. This is said to grow in a dorsal direction towards the position of the future anus, and in MASTERMAN's fig. 39 (Pl. III) it is represented as traversing the coelom, and being covered throughout by peritoneum. In the "transverse" sections shewing the stomach and intestine given in the same paper (figs. 54—56) these parts are in close contact with one another and appear to be suspended in a common peritoneal sac, formed by the inner walls of the two third body-cavities; and except in fig. 55 there is no indication that the peritoneum extends between them. If MASTERMAN's account is correct, it must therefore be supposed that the intestinal limb of the alimentary canal, after passing along the mesentery at a certain distance from the stomach, comes into contact with the posterior wall of the stomach as it travels towards the dorsal border of that organ. This, as a matter of fact, is precisely the arrangement which is found in the adults of all the species, and I was accordingly prepared to find that MASTERMAN's account of the formation of the intestinal flexure was correct. But the evidence seems to be opposed to MASTERMAN's statements. The intestinal limb, at its first origin, is enclosed in a peritoneal sac common to it and the stomach (figs. 170, 171; 56), and it becomes separated from the other limb of the alimentary canal only when it has passed the stomach and has become the rectum. In this position the intestinal limb has a peritoneal investment of its own, even in comparatively young buds; but I can find no evidence in the young stages of any trace of body-cavity in the concavity of the bend of the alimentary canal, as represented in MASTERMAN's fig. 39. The arrangement found in the adult must therefore be acquired at a later stage in the budding, and I imagine that what takes place is that the splanchnic epithelium of the

coelom (cf. fig. 171) grows in between the stomach and the intestine from either side until the two layers come into apposition and form a median mesentery. The stomach and intestine are separated, at the principal flexure of the gut, by a section of body-cavity in the advanced bud shewn in fig. 181. It is perhaps significant that this is found at the end of that part of the alimentary canal which still retains, in this bud, what may be regarded as the primitive antero-posterior direction. It is thus not impossible that the intervention of the body-cavity at this point only of the flexure has some morphological importance in indicating the region at which a dorsal flexure of the alimentary canal was first initiated.

I have but few observations on the later stages in the budding. In a bud in which two pairs of arms have developed their terminal knobs, I find that the ventral mesentery has already acquired its adult arrangement in the stalk, where its middle portion has broken down, leaving merely the anterior and posterior mesenteric ridges which support the corresponding stalk-vessels. Figs. 56—58 are sections transverse to the long axis of a bud of *C. gracilis*, and shew (*a*) that the ventral mesentery is incomplete in the region of the stomach in the buds of this species, as in the adult; (*b*) that the stomach and intestine are invested in a common peritoneum, the intestine only acquiring a coelomic covering on its axial or dorsal side when it becomes the rectum; (*c*) that the dorsal vessel originates by two lateral roots which are formed by folds of the splanchnic mesoderm covering the stomach, which is probably surrounded by a system of vascular spaces between its own epithelium and that of the coelom. This origin of the dorsal vessel is also indicated in the sagittal section of *C. dodecalophus* shewn in fig. 181.

Fig. 59 shews a section of an advanced bud of *C. gracilis*, cut transversely to its long axis. The mesentery of the third body-cavities is complete at this level, although it breaks down in the middle immediately after the alimentary canal ceases to be visible in the sections. The pharynx and stomach run in a horizontal plane, as in fig. 181; the next section nearer the basal end of the stalk merely cutting the ventral wall of the stomach tangentially, while the next section nearer the dorsal surface shews the intestine, which has started from the posterior end of the stomach seen in fig. 59.

The two collar-cavities (*b. c.*^{2}) are seen at the sides of the mouth (*m.*) the projecting lobes of the body-wall in which they lie being parts of the operculum. Between the operculum and the metasome, on the right side, is seen one of the collar-canals (*c. c.*), which appear to be formed, as MASTERMAN states (**98**, 2, p. 518), as derivatives of the ectoderm. The evagination (*g. s.*) of the pharyngeal wall seen on the right side can be identified as one of the gill-slits, from its relation to the collar-canal; and here too I am confirming one of MASTERMAN's results. The proboscis in this specimen is not lying symmetrically.

Fig. 5, of *C. levinseni*, is of interest as shewing that the proportions of the body, in young individuals of that species, are not unlike those of the adult *C. dodecalophus*.

XVII. DEVELOPMENT.

The observations which have hitherto been made on this subject are of the most fragmentary nature. The "Challenger" specimens of *C. dodecalophus*, although containing numerous eggs, each enclosed in a vitelline membrane and lying freely in the cavity of the coenoecium, were obviously obtained at a period shortly before the normal developmental season, and nearly all the eggs are unsegmented. MASTERMAN's observations (**98**, 2, p. 513) have already shewn, however, that some of the eggs are developing; and I have myself found several embryos.

The preliminary note published by ANDERSSON (**03**) shews that the embryos leave the parent colony in the form of ciliated "planulae". In the absence of evidence to the contrary, it may be presumed that ANDERSSON's statements refer to *C. dodecalophus*, since the larvae were obtained from material dredged in the Beagle Channel. The date on which the dredging was made was Oct. 30, whereas the "Challenger" material, in which development has hardly commenced, was collected on Jan. 11.

My own observations on the development have been made on *C. levinseni* and *C. gracilis*, in both of which the coenoecium contains embryos in various stages of development. My examination of this material has been incomplete, partly owing to the difficulties of staining — which are no doubt the result of imperfect preservation — and partly owing to the fact that I have not felt myself justified in sacrificing more than a small portion of the unique material, in each case, in order to study the development. The following statements with regard to this subject may, however, be made: —

(I) The egg of *Cephalodiscus* contains a large quantity of yolk.

(II) Segmentation is complete, although the later stages are influenced by the presence of yolk.

(III) The embryo leaves the colony at a comparatively early stage. This has been definitely observed by ANDERSSON, whose results are confirmed — so far as the negative evidence is worth anything — by the absence of later stages in the coenoecium of the specimens at present under consideration.

(IV) The structure of the oldest embryos observed makes it probable that development is direct, and that there is at no time any transparent, pelagic, larval stage.

(V) The embryos of the two species observed differ widely from one another in general appearance, but agree in essential features.

(VI) The body-cavity occurs in a completely segmented form before the time of hatching.

(VII) The alimentary canal, in the latest stages observed, has the character of a mass of yolk.

It is unfortunate that even the oldest embryos do not appear to throw any light on the way in which most of the organs of the adult are developed; and much remains to be done in the study of the development of the Pterobranchia.

All the developmental stages which have been observed are still enclosed in the vitelline membrane. *C. gracilis* and *C. levinseni* have a simple spherical or ovoid vitelline membrane, which is not prolonged into the narrow stalk found in *C. dodecalophus*.

(*a*) Embryos of *C. levinseni*.

The oldest embryos (Pl. XIV, figs. 198, 199) usually have an ovoid form, their greatest length being about 550 μ. The most striking facts which can be made out in the entire embryo are: — (I) that the yolk is practically confined, at this stage, to a central mass, which is distinctly divided into two regions; (II) that a large area of the ectoderm of one surface of the embryo is composed of cells which stain more readily than their neighbours; (III) that a part of the ectoderm near this differentiated region contains numerous, highly refractive, rod-like bodies.

Several frontal sections through an advanced embryo are shewn in Pl. XIV, figs. 207—210. It can hardly be doubted, from an inspection of these figures, that the region (*vac.*) containing the refractive bodies is the anterior end of the embryo. The part indicated above by (II) appears to be the ventral side, and I shall speak of it as the "ventral thickening" (*v. t.*). Its general shape is shewn in fig. 207, which is a frontal section cutting the whole of this "ventral" region. The subsequent sections (figs. 208, 209) shew that the ventral thickening extends round the anterior end of the embryo towards the dorsal surface, but that it disappears before it reaches that surface.

Figs. 203—205, from a transverse series, shew more of the characters of the ventral thickening, which contains a large proportion of much elongated cells of a glandular appearance. This tissue closely resembles that which composes the anterior, thickened wall of the proboscis of the adult. In both cases, the elongated gland-cells constitute the greater part of the epithelium, and moreover have exactly similar staining properties. Thus the gland-cells, of the adult proboscis and of the embryonic ventral thickening alike, stain intensely with HEIDENHAIN's haematoxylin or with "Orange G". It accordingly appears probable that the ventral thickening of the embryo is in some way converted into the glandular epidermis of the proboscis of the adult. If this be the case, it may perhaps be inferred that the embryo comes to rest, after a short free-swimming period, and secretes the commencement of the future coenoecium by means of the gland-cells in question.

The view just indicated with regard to the further history of the ventral thickening receives further support from the embryo represented in fig. 200. The part (*vac.*) containing the refractive bodies is much elongated, a condition which appears to be due to the fact that the embryo is squeezed into a narrow space between a zooid and the wall of its tube. The ventral thickening is closely applied to this wall, in a way which suggests that the embryo was crawling on it. The resemblance of these parts of the embryo to the proboscis of the adult is very striking, and it is rendered more significant by the fact that the free dorsal and lateral edge of the adult proboscis (Pl. I, fig. 5) contains refractive bodies somewhat similar to those of the embryo, although not behaving in quite the same way with varying modes of illumination.

The yolk-containing central mass of these embryos has a highly characteristic form, which may be described as umbrella-shaped (figs. 198—201). Distinct indications of a central cavity may be found in the median part of this mass (figs 198, 199), which is sharply marked off from the anterior part by the absence of yolk-globules in the intervening tissue. The whole of the rest of the umbrella-shaped central mass is crammed with numerous yolk-globules, which have a diameter of about 3—4 μ.

The general structure of the embryo may be illustrated by figs. 207—210. Fig. 207 shews practically the whole extent of the ventral thickening (*v. t.*). It consists of numerous gland-cells, cut transversely, and stained intensely with iron-haematoxylin, separated from one another by epidermic cells which are practically unstained. Posterior to the ventral thickening is a deep median groove which may be traced through a number of sections until it reaches the posterior end of the embryo (fig. 209). It is one of the characteristics of the older embryos found within the coenoecium that the epidermis is a good deal folded (fig. 210). It is thus not easy to decide whether the invagination shewn in fig. 207 is more than an unimportant fold. It does not appear, in the corresponding position, in figs. 205, 206, which may however belong to a younger embryo. But in the embryos of *C. gracilis*, a definite invagination (figs. 189, 190, *post. p.*), which may be termed the "posterior pit", occurs at the posterior end. The fold shewn in figs. 207—209 may provisionally be referred to under the same name.

Fig. 208 still cuts the ventral thickening, and shews on the right side a few of the refractive bodies which have already been noticed. The central yolk-mass is dilated in front and narrower behind, the posterior portion being surrounded by a space which appears to be blastocoelic in nature. The body-cavity consists of the five divisions characteristic of the adult. The collar-cavities (*b. c.*^{2}) lie externally to the blastocoelic spaces just mentioned, that of the left side being specially sharply marked, although both of them are quite definitely separated from the anterior body-cavity. The posterior body-cavities (*b. c.*^{3}) are seen on either side of the posterior pit.

It is not possible to decide from this section whether the proboscis-cavity possesses an epithelium or not. A clear space external to its cavity is due to the fact that the gland-cells of the ventral thickening do not extend quite through the thickness of the epidermis. The collar-cavities and the metasomatic cavities have indications of nuclei internally to the membrane which forms their outer boundary. The left metasomatic cavity contains posteriorly a mass of cells which has the appearance of being a definite organ.

In fig. 209 the ventral thickening is disappearing, and the ectoderm of the anterior end has the vacuolated appearance which is characteristic of the region containing the refractive bodies. Examined with a higher power, these appear to be rod-like accumulations of pigment-like granules. The posterior part of the ectoderm is not vacuolated. The umbrella-like character of the yolk-mass is very obvious. The anterior part is separated from the more axially placed mass by a region in which yolk-spherules are absent, or are present in very small numbers. This region is bisected, on the left side (and throughout, in other specimens favourable for the examination of this point), by a distinct line which may probably be regarded as part of the posterior boundary of the anterior body-cavity. The collar-cavities are distinct, while the posterior body-cavities are separated from one another by an obvious mesentery. There are still indications of a a blastocoelic space surrounding the yolk, and limited externally by the splanchnic membrane of the second and third body-cavities.

In fig. 210, the yolk-mass is continuous with the epidermis. This may be regarded as, in all probability, representing the blastopore and at the same time the future anus. The axial part of the yolk contains a cavity. This appears to be the enteric cavity, although neither here

nor in any of the other embryos is there the slightest indication of the differentiation of a digestive epithelium. The section passes on the dorsal side of the communication between the axial mass and the anterior yolk, which thus appear separate from each other. The intervening tissue, which is in the main free from yolk-spherules, shews part of the membrane which has already been mentioned. The anterior part of the ectoderm consists of vacuolated cells with refractive bodies, while the posterior two thirds is a good deal folded and consists of unvacuolated cells which appear to be provided externally with long cilia. The posteriorly directed fold of the collar-epidermis on the right side of fig. 210 cannot certainly be differentiated from the other folds of the epidermis which are characteristic of the older embryos. But as a precisely similar fold appears, a few sections further, on the other side of the embryo, with a similar relation to the left collar-cavity, I am inclined to regard it as of some significance.

Figs. 104—106 (Pl. IX) are taken from a sagittal series of sections. Fig. 104, which belongs to the lateral region of the embryo, shews the two transverse septa between the body-cavities. Fig. 105 shews that not only is the posterior limit of the anterior body-cavity prolonged into the yolk-mass as a region traversed by a definite line and free from yolk, but that a similar yolk-free region corresponds with the division between the second and third body-cavities. This is the case on the dorsal side at least. On the ventral side it is not certain that the collar-cavity exists. The ventral thickening resembles the anterior epidermic thickening of the adult proboscis in the fact that the gland-cells are separated from the basement-membrane by a homogeneous layer which in the adult has been interpreted as part of the epidermic nerve-plexus. The dorsal posterior part of the epidermis is obviously ciliated in the section from which fig. 105 was drawn.

In fig. 106, which is nearly median, the third body-cavity can be recognised both dorsally and ventrally to the intestinal region, while the collar-cavity can only be made out dorsally. This section shews the edge of an invagination (*s. o.*) of the dorsal vacuolated ectoderm of the anterior end, which forms a conspicuous organ better seen in the series next to be described.

Figs. 202—206 represent five sections taken from a transverse series of sections of an advanced embryo, stained with haematoxylin and Orange G. Fig. 202, through the anterior end, shews the front part of the ventral thickening, the gland-cells of which, like those of the adult proboscis of specimens treated in the same manner, are intensely coloured with the orange stain. The dorsal vacuolated ectoderm, in which some of the refractive bodies are seen, projects inwards in the form of a rounded organ (*s. o.*) which has the appearance of a series of large vacuoles separated by trabeculae coloured with haematoxylin. A crescentic section of the anterior body-cavity (*b. c.*[1]) adjoins this organ, while the other space seen in the section is shewn, by comparison with other specimens, to be external to the basement-membrane (*b.m.*) of the epidermis, and may be artificial. Part of this space remains at the base of the ventral thickening in fig. 203, in which is seen the anterior part of the yolk, in the middle of which is an interval free from yolk-spherules and traversed by a distinct line. This is the extreme anterior part of the division between the two parts of the yolk shewn in fig. 210. The yolk-spherules are intensely stained with Orange G, and the whole mass is surrounded on all sides by the anterior body-cavity, in

the somatic wall of which there are some indications of an excessively thin epithelial lining. The dorsal ectoderm, which has taken, in the main, the haematoxylin colour, still shews at its base remains of orange-coloured yolk-spherules. It further contains a certain number of vacuolated structures, stained with haematoxylin, and similar to those which compose the organ *s. o.* seen in fig. 202. These structures may probably be regarded as gland-cells. The rest of the ectoderm consists of closely packed narrow cells. In fig. 204 the yolk-free region in the middle of fig. 203 has extended as an elliptic line through the yolk-mass, which is thus divided into a central and a peripheral portion. The former surrounds a split-like cavity, which may be regarded as the commencement of the future alimentary canal. The ectoderm no longer contains any gland-cells. On one side of the section is a narrow space (*b. c.*) lined by an obvious epithelium. This appears to be one of the collar-cavities, although the series of sections is not suitable for distinguishing between the second and third body-cavities in the more posterior parts of the embryo. It is, however, probable that in fig. 205 the ventral mesentery is that of the third body-cavities, while the septum between these and the collar-cavities is not visible. I have assured myself that in some of the embryos adjacent body-cavities may appear continuous as the result of defective preservation. It can hardly be doubted that in the embryo here represented the paired body-cavities have a splanchnic lining as well as the more distinct somatic lining, but there is no evidence of the existence of a splanchnic layer in the region of the anterior body-cavity.

The last remains of the anterior yolk-mass are seen in fig. 206, a few sections beyond which the posterior yolk-mass becomes connected with the epidermis by the divergence from one another of the two laminae of the ventral mesentery. In the more posterior sections a dorsal mesentery seems to be indicated, in addition to the ventral mesentery.

The consideration of figs. 203—206 shews that in this embryo the anterior body-cavity sends a median prolongation backwards, on the dorsal side of the yolk, between the halves of the paired cavities. A similar arrangement is shewn in fig. 201, an obliquely longitudinal section, in which although the three segments of the body-cavity are seen with moderate certainty on the dorsal side (left of figure), it is not quite certain that the collar-cavity is represented on the ventral side.

(*b*) Embryos of *C. gracilis*.

The oldest embryos of this species have the form represented, in side view, in fig. 188. The embryo here shewn measures 300 μ. in length, and like all the other embryos, both of this species and of *C. levinseni*, it is still enclosed in the vitelline membrane. Its most conspicuous organ is a large invagination of ectoderm (*v. inv.*), on what may be regarded as its ventral side. At the anterior end is a median organ (*s. o.*) characterised by its transparency, while at the opposite end is a median depression of the ectoderm (*post. p.*). In the interior of the embryo is a mass of yolk, which can be seen to be composed of two portions separated by an indentation. The refractive bodies characteristic of the anterior end of the embryos of *C. levinseni* do not occur, or at least not in precisely the same form. They may, however, be represented by cells containing a brownish pigment which are scattered irregularly throughout most of the ectoderm, though found in somewhat larger numbers near the posterior pit.

Other embryos have a more spherical form, as for instance that shewn in fig. 187, a view from the ventral and anterior sides. The anterior transparent organ (*s. o.*) is indicated externally by a depression, while the orifice of the ventral invagination is very conspicuous.

Fig. 189 represents a spherical embryo seen from the ventral side, some of the organs being shewn in optical section. It is probably somewhat older than fig. 187, the aperture of the ventral invagination being considerably shorter from before backwards than in that specimen. An emargination occurs in the outline at each end of the sagittal plane of the embryo, representing respectively the transparent organ (*s. o.*) and the posterior pit (*post. p.*). These emarginations are even more conspicuous in the younger stages.

The most striking difference between these embryos and those of *C. levinseni* is due to the presence of the large ventral invagination in *C. gracilis*. It seems to me probable that this is the representative of the ventral thickening of the embryos of *C. levinseni*, and that it is to be regarded as a ventral flexure, comparable with that of the embryos of other animals which undergo part of their development within an egg-membrane. It may be supposed that with the escape of the embryo from the vitelline membrane, the ventral invagination will flatten itself out and the embryo will thereby assume a more elongated form.

Fig. 197 is a sagittal, nearly median section of an advanced embryo of *C. gracilis*, shewing the transparent organ (*s. o.*), the ventral invagination (*v. inv.*) and the edge of the posterior pit (*post. p.*). The internal yolk-mass has an emargination dorsally, in which lies a well marked coelomic vesicle (*b. c.*^{2}). It can hardly be doubted that this represents the collar-cavity, and accordingly that the undivided space (*b. c.*^{1}) in front of it is the anterior body-cavity, while the spaces (*b. c.*^{3}) at the opposite end are the third body-cavities. Both the right and the left cavity, with the ventral mesentery, are here seen, in consequence of a slight obliquity of the section. The anterior third of the ectoderm, between the two arrows shewn in the figure, is vacuolated in this embryo, while the remainder of the ectoderm is composed of narrow, closely packed epithelial cells of considerable height.

Figs. 190, 196, 195 are three horizontal sections of a similar embryo. Fig. 190, which shews some histological detail, passes through the dorsal end of the ventral invagination (*v. inv.*) the epithelium of which is cut tangentially; and the lumen of the organ is thus not seen. Rather more than half of the ectoderm, at the anterior end, has a vacuolated structure, resembling that of the same part in *C. levinseni*. The rest of the ectoderm is composed of narrow, closely packed cells. In all parts of the ectoderm, except in the anterior transparent organ, occur the pigmented cells noticed in the entire embryos. There is some indication, in this and in other cases, that an accumulation of the pigment occurs on either side of the organ *s. o.* There is distinct evidence that rounded masses of the pigment are passed to the outer side of the ectoderm, where they are found within the vitelline membrane (fig. 197, *exc.*), an observation easily made both in sections and in entire embryos. It may naturally be suggested that this embryonic pigment is of excretory nature; a conclusion which perhaps carries with it the consequence that the refractive bodies found in the embryos of *C. levinseni*, and moreover the epidermic pigment of the adult *Cephalodiscus*, may have the same physiological value.

The transparent organ (*s. o.*) has a pear-shaped outline, and consists of a highly vacuolated

tissue traversed by excessively fine threads containing a few minute nuclei. The organ is connected laterally with a part of what appears to be an epidermic nerve-plexus. This (*n. t.*) is seen on the right side of fig. 190, but it is seen also on the left side in other sections of the same embryo. The intimate connexion of the transparent organ with the embryonic nervous system suggests that the organ itself is a sense-organ; and both in structure and in its relation to the nervous system it recalls the "pyriform organ" of the larvae of Ectoproct Polyzoa: — a resemblance which need not indicate any affinity of *Cephalodiscus* to the Polyzoa [1]).

The five coelomic spaces of *Cephalodiscus* are probably indicated in fig. 190. The proboscis-cavity (*b. c.*[1]) has a somatic epithelium, in its anterior part at least, but I find no evidence of the existence of a splanchnic layer. The collar-cavity (*b. c.*[2]), on the left side, has a form and position which appear to be very characteristic of this species. It is somewhat triangular in section, with its base applied to the ectoderm and its apex projecting into the emargination of the yolk. On the right side (which passes through a more ventral region than does the left side of the section), the collar-cavity is a small oval vesicle, lying more posteriorly than the corresponding left cavity. A similar difference is noticeable in the third body-cavities, the section cutting the lumen of the left cavity and the ventral wall of the right cavity.

Fig. 196 represents a more dorsal region of the same embryo. It involves the dorsal end of the posterior pit, which in this embryo has the form of a vertical slit, and it shews the five body-cavities. The manner in which the paired cavities end ventrally has not been ascertained with certainty, but it seems that the trunk-cavities are separated by a ventral mesentery, as in fig. 197.

Fig. 195 appears at first sight to indicate that the two collar-cavities become continuous with one another in the middle dorsal line. The sections are, however, not accurately horizontal, and an examination of the neighbouring sections leads to the result that the cavity seen in fig. 195 is really the dorsal end of the right collar-cavity.

Figs. 191—194 illustrate the structure of an advanced embryo as seen in transverse sections. Fig. 191 shews the anterior sense-organ (*s. o.*), on either side of which is a mass of what seems to be nerve-tissue (*n. t.*). The dorsal two thirds of the ectoderm is composed, as is usual in embryos at this stage, of vacuolated cells. In the next section further back (not drawn) the nerve-tissue can be seen underlying the ventral ectoderm, while in later sections (figs. 192—194) it underlies the greater part of the ectoderm, wherever this layer has assumed the form characterised by the absence of conspicuous vacuoles. There is in fact, in this embryo, a general epidermic nerve-plexus similar to that of Balanoglossus. There appears to be a slight concentration of this plexus at the angle between the wall of the ventral invagination and the lateral ectoderm (fig. 192). A ventral nerve is perhaps visible in fig. 193.

The ventral invagination consists partly of vacuolated cells, intermingled with the narrow

1) It might be possible to make a detailed comparison between the embryo of *C. gracilis* and that of one of the Ectoprocta, based on the similarity of the internal mass of undifferentiated yolk and on the pyriform organs of the two embryos, and comparing the ventral invagination of *Cephalodiscus* with the "internal sac" of the Ectoprocta. Believing as I do that the Ectoprocta are related to the Entoprocta, and that the larvae of the latter indicate affinities with other groups characterised by the possession of a Trochosphere larva, I am not at present prepared to admit that the embryology of *Cephalodiscus* suggests any affinity between that animal and the Polyzoa.

epithelial elements characteristic of the rest of the ectoderm, while a certain amount of substance which is faintly stained (with borax carmine) may represent the glandular cells of the adult proboscis. This substance occurs, in the present instance, mainly near the bases of the ectoderm-cells, although in another embryo it occurs in larger quantity throughout the ventral invagination, which has lost the vacuolated condition just noticed.

Some of the cells on the right side of the orifice of the ventral invagination in fig. 192 project individually to the exterior. By comparison with other sections of the same embryo, it appears probable that this is a stage in the evacuation of excretory products. Turning to the body-cavities, fig. 192 shews the anterior cavity, with a distinct somatic epithelium, while in fig. 193 are seen the second and third cavities. The collar-cavities (*b. c.*[2]) are separated from one another dorsally by a slight median thickening of the ectoderm, perhaps the commencement of the central nervous system. In their ventral region they pass round the outer borders of the posterior body-cavities, an arrangement which is also indicated in fig. 196. Both pairs of coelomic spaces are complete sacs, surrounded on all sides by an epithelium. In fig. 194 the collar-cavities have disappeared, while the posterior coelomic sacs seem to be continuous ventrally with the yolk.

It would undoubtedly be possible to obtain fuller information with regard to the early development of *Cephalodiscus* from the material at present at my disposal; but I have refrained from sacrificing more than a small quantity of the specimens in order to study this subject. It is moreover highly probable that satisfactorily preserved material will soon be forthcoming, as is indicated by the short statement that has recently been published by Andersson (**03**). The examination of these heavily yolked eggs and embryos would undoubtedly be facilitated by the employment of specimens preserved by suitable histological methods. The history of the development, so far as I have been able to follow it, by means of the embryos described above, together with the few earlier stages I have examined, may be summarised as follows.

(I) The egg is large (300—400 μ. in greatest length) and is richly provided with yolk. It becomes surrounded by a vitelline membrane on passing into the cavity of the coenoecium, and it remains inside this membrane during the whole of the earlier stages of its development. The embryo is probably hatched at the stage represented by figs. 188, 198—200 (cf. Andersson, **03**).

(II) Segmentation is complete. Fig. 186 *(C. gracilis)* shews the first cleavage, one of the blastomeres being apparently preparing for a second division. Masterman (**98**, 2, p. 514, Pl. V, fig. 89) describes an embryo which, according to his statement, is a larva divided into two segments by a more or less equatorial furrow. Although I do not wish to dispute the accuracy of this statement, there is nothing in Masterman's account to forbid the supposition that the figure might represent an egg divided into two blastomeres.

I have found one or two late segmentation stages, from which the only conclusions I can certainly draw are that the cleavage continues to be complete, and that it gives rise to a solid embryo.

(III) The solid embryo just indicated consists of numerous cells, a large number of which are internal. The formation of the inner layer appears to take place by a process of delamination,

the externally placed cells differentiating themselves off as an ectoderm, while the central mass gives rise to the yolk-mass of later embryos, and probably to the coelomic spaces.

(IV) Immediately after the differentiation of the ectoderm, the yolk is equally distributed throughout the embryo. It now disappears from the ectoderm, and in the later stages is found entirely in the large yolk-mass which occupies the greater part of the cavity.

(V) The yolk-mass becomes constricted, in front of the middle *(C. levinseni)* or behind the middle *(C. gracilis)*. The anterior part projects backwards over the posterior part as an umbrella-shaped mass of yolk, specially noticeable in *C. levinseni*. There is practically no sign of histological differentiation in the yolk-mass at any stage observed, although a cavity, probably the future enteron, appears in the posterior part of the yolk *(C. levinseni)*.

(VI) The ectoderm undergoes a considerable amount of histological differentiation.

(*a*) The antero-dorsal portion becomes highly vacuolated, and at its front end a larval sense-organ is formed. In *C. gracilis* this is a sharply marked pear-shaped organ (fig. 190, *s.o.*), which reaches the exterior at the base of a slight depression of the surface, while in *C. levinseni*, the organ is connected with a more definite invagination of the anterior ectoderm. It is not impossible that this sense-organ may represent the similar organ found in *Tornaria* (cf. MORGAN, **94**, p. 33, Pl. III, fig. 19). The anterior vacuolated ectoderm in *C. levinseni* contains numerous refractive bodies, while in *C. gracilis* nearly the whole of the ectoderm contains scattered pigment-masses (fig. 190) which are probably excretory, since their occurrence between the vitelline membrane and the epidermis indicates that they are discharged to the exterior.

(*b*) The anterior half or more of the ventral ectoderm, in *C. levinseni*, is somewhat thickened and forms a glandular mass, described above as the "ventral thickening". This tissue stains in the same way as the thickened glandular epidermis of the anterior side of the adult proboscis, and it may probably be identified with this part of the adult animal. In *C. gracilis*, the corresponding part of the embryo forms a conspicuous "ventral invagination", which is probably due to a flexure of the embryo within its vitelline membrane.

(*c*) At the posterior end of the embryo is a vertical slit-like invagination, or "posterior pit" in *C. gracilis* (figs. 188—190); while in *C. levinseni* (figs. 199, 207—209) there appears to be a longer slit-like groove exending from the posterior end along part of the ventral surface of the embryo.

(*d*) The remainder of the ectoderm, in both species, consists of much elongated, very narrow cells. Distinct evidence that these are ciliated was obtained in some cases (fig. 210). In the older embryos of *C. levinseni*, the ectoderm becomes folded in a complicated way. An early stage in this process is shewn in fig. 210, but in older embryos the folds acquire a much greater degree of complexity.

(VII) The body-cavity is represented by five coelomic spaces, corresponding with those of the adult. The proboscis-cavity may have distinct indications of a somatic epithelium, but there is no proof that a splanchnic layer is present. The second and third cavities, on the contrary, are probably sacs with a complete epithelial investment. The origin of the coelomic spaces has not been traced.

While the embryos described above shew obvious indications of possessing the essential structure of *Cephalodiscus*, the clue to the precise relations between embryo and adult will probably be furnished by the study of the later stages, which are not yet forthcoming. The consideration of the embryo of *C. levinseni* shewn in fig. 200 suggests that the ventral thickening can be used as a crawling organ, and that it is probably already in a condition to secrete the commencement of the coenoecium. The absence of a functional alimentary canal further points to a free life of brief duration, and it appears probable that the larva constructs its tube after a very short free life, and undergoes an important part of its metamorphosis within its tube. The very striking folding of the ectoderm in the old embryos of *C. levinseni* is perhaps a preparation for the stretching of the body-wall necessary to provide accommodation for the future alimentary canal, the anal region of which appears to be indicated in fig. 210.

One of the points which appears to be most problematical in the structure of the embryos is the meaning of the anterior umbrella-like mass of yolk. It is conceivable that in the rearrangement of the viscera which presumably accompanies the metamorphosis, it might give rise to part of the anterior end of the alimentary canal. That conclusion seems to be improbable if the part in question is really in front of the collar-cavities (cf. figs. 209, 210).

Another possibility which must not be left out of account is that the embryo undergoes no metamorphosis, but that it may fix and give rise to the adult zooids by budding. A process of this kind is characteristic of the great majority of Ectoproct Polyzoa, in which (with rare exceptions) the alimentary canal of the free larva is represented by at most a mass of yolk-like material, as in *Cephalodiscus*. Although this possibility can hardly be excluded, it seems to me that the embryos of *Cephalodiscus* possess sufficient indication of the adult organs — and particularly of the body-cavities — to make it probable that the embryo undergoes a metamorphosis into a zooid.

It is not impossible that the umbrella-like mass of yolk represents in itself the splanchnic epithelium of the anterior body-cavity. While the paired cavities, in some of the specimens at least, are unmistakeably complete coelomic sacs, I have not been able to convince myself in any case that the anterior body-cavity has a splanchnic epithelium distinct from the yolk-mass itself. I am in fact inclined to accept this explanation as the most likely one which can at present be given. This interpretation is in accordance with the account given by Bateson (**84**, p. 218) of the development of *Dolichoglossus kowalevskii*, a species of Balanoglossus in which the development is direct. It appears from Bateson's account that the entire front end of the archenteron is separated off as the anterior enterocoel, the walls of which overlap the axial enteron in precisely the same manner, though to a less extent, as the anterior yolk overlaps the posterior yolk in *Cephalodiscus levinseni* (cf. Bateson's figs. 35, 40, 27, 28). There are indeed differences in detail between the two cases. Thus in Balanoglossus, the somatic layer is as thick as, or thicker than, the splanchnic layer, while in *Cephalodiscus* the somatic wall is excessively thin, and at first barely recognisable, while the splanchnic layer is, ex hypothesi, constituted by the thick yolk-mass itself. Again, while in Bateson's larva, the anterior enterocoel communicates at first with the enteron, in *Cephalodiscus* the whole complex forms a solid mass of yolk without any cavities.

If it be permitted to appeal to animals which though less nearly related to *Cephalodiscus* are still, as it appears to me, possessed of affinities to Balanoglossus, allusion may be made to Amphioxus and Echinoderms, in support of the explanation given above of the structure of the embryo of *Cephalodiscus*. The anterior body-cavity of Amphioxus, as described by HATSCHEK, is developed from the anterior end of the original archenteron, and shortly before its separation from the mesenteron it forms a cavity projecting backwards beyond the anterior end of the mesenteron in much the same manner as that in which the anterior yolk-mass of *Cephalodiscus* overlaps the remainder of the yolk. A similar arrangement has been described in many Echinoderms, as by LUDWIG and MACBRIDE in *Asterina*, by MASTERMAN [1]) in *Cribrella*, and by MACBRIDE [2]) in *Echinus*.

The characteristic relation of the collar-cavities in the embryo of *Cephalodiscus* to the constricted region of the yolk makes it by no means improbable that these cavities are true enterocoels, given off from the archenteron in this region; while fig. 194 appears to suggest that the third body-cavities have a definite relation to the posterior end of the yolk-mass. It is not impossible that the somatic epithelium of the paired body-cavities is first differentiated at the surface of the yolk, and that the splanchnic epithelium gradually spreads round the yolk-mass in the manner which might be indicated by the posterior end of fig. 201. Against this view may be set the fact that the paired coelomic spaces, at the earliest stage at which they have been recognised, appear to be separated from the yolk by a distinct membrane (figs. 208, 209), even though no epithelial lining can be detected on the outer side of this membrane.

The general arrangement of the coelomic spaces in the embryo appears to me to have a close resemblance to that shewn by BATESON in his well known diagram (**84**, Pl. XXI, fig. 40) of the embryo of *Dolichoglossus kowalevskii*, with the exception of the fact that the archenteron is represented, in *Cephalodiscus*, by a practically solid mass of cells.

XVIII. AFFINITIES.

In 1887 I had the opportunity of bringing forward evidence tending to shew that *Cephalodiscus* must be placed in the same group with Balanoglossus. I indicated at the same time my belief that it might have affinities with *Phoronis*, though not with the Polyzoa. It appeared to me not improbable that *Rhabdopleura* was related to *Cephalodiscus*, as had been assumed from the first by M'INTOSH, LANKESTER and others; but in view of the want of evidence with regard to the structure of *Rhabdopleura* I refrained from expressing a definite opinion on this part of the question.

The subject of the affinities of *Cephalodiscus* has aroused a good deal of interest in recent years. It may conveniently be considered under several headings, as follows: — namely the affinity of *Cephalodiscus* to:

1) Trans. Roy. Soc. Edinburgh, XL, Pt. 2, 1902, p. 385 f.
2) Phil. Trans. Roy. Soc. London (B), CXCV, 1903, p. 296.

(I) *Rhabdopleura.*
(II) Enteropneusta.
(III) *Phoronis.*
(IV) other animals.

(I) Relations to *Rhabdopleura.*

The researches of FOWLER (**92**, 1, 2; **04**) and of SCHEPOTIEFF (**04**) appear to me to have demonstrated the correctness of the opinion expressed by the earliest investigators of *Cephalodiscus* (M'INTOSH, **87**, pp. 1, 32) that this animal is most nearly related to *Rhabdopleura*. It is true that FOWLER's results have been criticised by MM. CONTE and VANEY (**02**) whose conclusions have been published in the form of preliminary communications only. They have been replied to by FOWLER (**04**), but in the absence of the full memoir it is difficult to do justice to the results of the French authors. The most important of their statements are perhaps (*a*) that the body-cavity of *Rhabdopleura* is not subdivided in the way characteristic of *Cephalodiscus*; (*b*) that the testis has the form figured by LANKESTER (**84**, Pl. XL, fig. 7) and that it is formed from "une différentiation de l'extrémité antérieure du pédoncule"; while the ovary, described for the first time, is formed at the expense of the axial part of the peduncle, "mais "à l'extrémité opposée à celle où se développe le testicule"; (*c*) that collar-canals do not exist; (*d*) that the notochord is merely the anterior part of the peduncle; (*e*) that *Rhabdopleura* is related to the Entoproct Polyzoa.

The denial of the existence of the notochord, collar-canals and subdivisions of the body-cavity is directly opposed to the results of FOWLER, which appear to me to be reliable. I have satisfied myself of the existence of the collar-canals at least, although I have had but little material suitable for the examination of the structure of *Rhabdopleura*. SCHEPOTIEFF (**04**) with a knowledge of the statements of CONTE and VANEY has, moreover, confirmed FOWLER's results in essential particulars, although he considers (p. 16) that the cavity of the two arms is not continuous with that of the rest of the collar, and he alludes to the collar-canals (p. 15) as "Nephridien". One point in the results of MM. CONTE and VANEY is of special interest in connexion with *Cephalodiscus*, namely the account of the gonads and particularly of the testis. The statement that that organ is a differentiation of the axial part of the stalk may well have some relation to the phenomena which I have described in *C. sibogae*. I do not profess to understand their statements with regard to the ovary.

If FOWLER's results, confirmed by SCHEPOTIEFF, may be accepted, it seems to me hardly possible to doubt that *Rhabdopleura* is the nearest known ally of *Cephalodiscus*. The subdivisions of the coelom and the corresponding external segmentation, the relations of the arms to the collar-region, the structure of the stalk, the phenomena of the budding, the existence of the notochord and collar-canals, all these form a cumulative body of evidence [1]) which appears to point conclusively in that direction.

1) In the copy of his paper which M. SCHEPOTIEFF has had the kindness to send me, he has added the following MS note "Ein Paar dorsalen Poren am Kopfschild wurden neulich gefunden".

(II) Relations to the Enteropneusta.

The resemblances of *Cephalodiscus* to Balanoglossus have been confirmed by several workers who have had the opportunity of studying sections of the former animal; and particularly by MASTERMAN (**96—03**) and SPENGEL (**93**, pp. 721, 753). LANG (**90**) has accepted the same conclusion, and has given reasons for regarding *Cephalodiscus* as a Balanoglossus-like form which has been specially modified in connexion with its sedentary and tubicolous habits. EHLERS (**90**, p. 164) on the contrary denied the affinity of *Cephalodiscus* to Balanoglossus.

It seems to me hardly necessary to discuss this question further. If any weight is to be attached to morphological resemblances it must be concluded that *Cephalodiscus* is related to Balanoglossus. When account is taken of the differences between the external form, the size, and the habits of the two types, it is indeed extraordinary that so many of the anatomical peculiarities of Balanoglossus should reappear in *Cephalodiscus*. As facts confirming the relationship of the two forms, but not known at the time of the publication of the "Challenger" Report may be mentioned, — the existence of a pericardium, and probably of a glomerulus, in *Cephalodiscus*; the discovery, by MASTERMAN, of a vascular system in the same animal; and the resemblances of the embryos of *Cephalodiscus*, so far as I have been able to make out their structure, to those of *Dolichoglossus kowalevskii*.

It cannot, however, be disputed that in spite of the resemblances, *Cephalodiscus* differs from Balanoglossus in various particulars which are so obvious as not to require mentioning. But the general result seems to me clear, namely that *Cephalodiscus* and *Rhabdopleura*, constituting the Pterobranchia or Aspidophora, must be included, with the Enteropneusta, in a larger group, for which I accept BATESON's name Hemichordata.

(III) Relations to *Phoronis*.

Here we are on much more controversial ground. The hypothesis of the affinity of *Phoronis* to the Pterobranchia has been accepted by a certain number of authors, among whom I may mention LANKESTER (**85**), MASTERMAN (**96—00**), SCHIMKÉWITSCH (**93**), DELAGE and HÉROUARD (**97**), ROULE (**01**, p. 226), and SCHULTZ (**03**, 1, 2); but it has been rejected by many others. MASTERMAN's comparisons of Actinotrocha with *Cephalodiscus* and the Enteropneusta have unfortunately been vitiated by the mistakes into which he appears to have fallen with regard to the structure of Actinotrocha, as shewn by the concurrent testimony of IKEDA, GOODRICH, and DE SELYS LONGCHAMPS. SCHULTZ (**03**, 1, p. 414; **03**, 2, p. 489), while accepting the verdict of these authors with regard to the facts, believes nevertheless in the affinity of *Phoronis* to *Balanoglossus*, and expresses his conviction that evidence of this relationship is to be found more in the structure of *Phoronis* than in that of its larva. He bases his conclusions on the result of a study of the regenerative processes of *Phoronis*, whether after the spontaneous loss of the tentacular end of the animal or after artificial section; and on the study of regeneration in Actinotrocha after section. He finds that regenerative processes are capable of giving valuable aid in the elucidation of phylogenetic problems.

DE SELYS LONGCHAMPS (**04**) has just published an important memoir on the structure and metamorphosis of Actinotrocha. The full bibliography which he has given, and his careful

discussion of the opinions which have been expressed by various writers make it unnecessary for me to attempt the same task in all its details. I may therefore limit myself to comments on a few of the points which seem to me to need further discussion.

De Selys Longchamps concludes that *Phoronis* is not nearly allied to *Cephalodiscus*. He shews, with Ikeda and Goodrich, that Masterman's proboscis-cavities and collar-cavities in Actinotrocha are not distinct spaces, but that the body-cavity is divided into two parts only by the oblique septum which has universally been recognised as occurring at the base of the series of larval tentacles. He recognises, however, the fact pointed out by Ikeda and confirmed by Goodrich (**03**) and Schultz (**03**, 2) that at a somewhat late stage in the development of Actinotrocha, there originates a coelomic space which lies just in front of the larval septum and sends outgrowths into the permanent tentacles. In his discussion of the cavities of the body he does not seem to me to take enough account of the morphological importance of this space, the mode of development of which is, however, not quite certain. Goodrich (p. 111) and de Selys Longchamps (p. 33) consider that it is formed as a schizocoel, while Schultz (**03**, 2, p. 487, figs. 18, 19) states that in Actinotrocha, regenerating after injury, it arises as two anterior diverticula of the post-septal coelomic cavity. But, however it may first originate, authors are agreed in stating that it increases in relative size during the further development. At the metamorphosis, when a large part of the anterior region of Actinotrocha is thrown off, the remains of the praeseptal blastocoelic cavity persists as the vascular ring or rings, while the praeseptal coelomic space becomes the lophophoral coelom of the adult, giving rise also (Schultz, **03**, 2, p. 487) to the cavity of the epistome.

Schultz, with Fowler (**92**, 2, p. 297), considers that the praeseptal coelom is to be regarded as the homologue of the collar-cavity of the Enteropneusta; but he is of opinion that this Enteropneust feature is only acquired with the assumption of the adult characters, the larva having the significance of a Trochosphere, and not shewing any indications of "trimetamery". I am inclined to accept the view that the adult lophophoral cavity is a collar-cavity, but I think that the view of Schultz with regard to the significance of Actinotrocha requires some modification. It may be noted that although this author recognises the second and third body-cavities of the Enteropneusta in the adult *Phoronis*, he does not attempt to shew that there is any representative of the anterior body-cavity in that animal. My own view with regard to this point is intermediate between that of Masterman and that of Schultz.

De Selys Longchamps lays stress on the distinction between the haemocoelic nature of the large praeseptal cavity of Actinotrocha (which he nevertheless terms the "cavité collaire") and the coelomic nature of the metasomatic or postseptal cavity. It can hardly be doubted, from the relations of the larval blood-corpuscles, which lie freely in the praeseptal cavity and at the metamorphosis pass into the blood-vessels, that the cavity itself has intimate relations with the vascular system. But in the younger stages of Actinotrocha, the praeseptal cavity is continuous with the metasomatic cavity, the septum being differentiated first on the ventral side, and being completed dorsally only at a comparatively late stage in larval life. When the septum is complete, there is a postseptal coelomic cavity with a coelomic epithelium, and a praeseptal haemocoelic cavity which has no complete epithelial lining.

It seems to me that if, as DE SELYS LONGCHAMPS shews, the two cavities are continuous in the earlier stages it is difficult to assume that they differ from one another to quite so great an extent as is maintained by that author. Both cavities may in fact be said to be formed from the original blastocoel, the mesoderm cells in one case arranging themselves round the cavity so as to give rise to a coelomic epithelium, and in the other case not behaving in this manner. It must be remembered that at the metamorphosis of Actinotrocha, a considerable part of the anterior region of the body, including the praeoral lobe, is completely lost. The balance of evidence appears to be in favour of the view that the adult epistome is not a remnant of the praeoral lobe (cf. DE SELYS LONGCHAMPS, **03**, p. 42 and **04**, p. 73). If then the anterior region of the larva is not destined to give rise to an adult protomere (or proboscis), in consequence of the peculiar phenomena which occur at the metamorphosis, it is perhaps possible that it may have lost some of the characteristics of the protomere. The metasomatic cavity is admittedly indistinguishable from the blastocoel in the younger larvae. If this be conceded, I see no great difficulty in supposing that the cavity of the protomere of Actinotrocha remains in the same undifferentiated condition. The praeseptal cavity might thus represent not only the vascular space which it is shewn to be by actual evidence, but also the region in which the anterior body-cavity is potentially present. The praeoral lobe of Actinotrocha may thus possibly represent the protomere of the Hemichordata. The region in Actinotrocha between the praeoral lobe and the larval tentacles may represent the collar, as supposed by MASTERMAN, although the definitive formation of its coelom is deferred to a late period in ontogeny. DE SELYS LONGCHAMPS (**04**) throughout speaks of this as the "région collaire"; although, as he does not accept the homology implied by that term, it may be presumed that he uses it for descriptive purposes merely.

It is thus possible to imagine that in Actinotrocha, the anterior body-cavity never acquires its full development, while the collar-cavity develops late; and that the adult *Phoronis* has lost its proboscis, while its collar-region is represented by the praeseptal part of the body, including the lophophore and tentacles.

It is perhaps a fact of some significance that the cavities of Actinotrocha have a characteristic obliquity, the "trunco-collar septum", as DE SELYS LONCHAMPS calls it, extending much further forwards dorsally than ventrally. The same obliquity is visible in the lophophoral cavity which is developed late in larval life, since this rests on the anterior face of the main septum, a relation which is well shewn by GOODRICH (**03**, fig. 2). A similar obliquity of the coelomic cavities to the actual main axis of the animal is obvious in *Cephalodiscus*, and is shewn for instance in the sagittal section of a bud figured in Pl. XIII, fig. 174 of this Report.

If I am right in the explanation I have given in Sect. VIII (p. 30) of the morphology of the arms and operculum of *Cephalodiscus* (cf. Pl. III, fig. 25; Pl. XII, figs. 158—160), the entire anterior border of the collar of that animal is prolonged into a free fold, with the exception of two lateral regions where there may be an interruption in the fold, and of the mid-dorsal region. The ventral half of this fold is constituted by the operculum, and the dorsal half by the tentaculiferous arms. If the lophophore of *Phoronis* belongs to a region which is morphologically comparable with the collar of the Hemichordata, it may be suggested that its tentacles should be compared not merely with the arms of *Cephalodiscus*, but with the whole

of the anterior edge of the collar in that animal. In other words, the operculum must be taken into account, as indeed I formerly suggested (**87**, p. 46), although in *Cephalodiscus* this region has not been split up into arms or tentacles. In constructing a diagram to shew the actual anatomical relations of the arms and operculum in *Cephalodiscus*, I arrived at the result seen in fig. 159. This diagram is supposed to represent an individual in which the proboscis was directed forwards (as in fig. 23), the proboscis itself having been cut away with the exception of the part which is present in the proboscis-stalk. The operculum is further supposed to have been stretched so as to pass completely externally to the series of arms, instead of being partially concealed by their bases in the way shewn, in a dorsal view, in fig. 158. The free anterior edge of the collar thus forms a funnel leading to the mouth, incomplete dorsally, and elongated in a transverse direction, the lateral parts being reflected towards the dorsal side. This diagram, constructed without any theoretical bias, has considerable resemblances to figures of the lophophore of *Phoronis*, for instance to those given by BENHAM (**89**, Pl. X, figs. 12, 7). It is indeed possible that the interruption, in the mid-dorsal line, of the series of tentacles described by BENHAM and other authors in *Phoronis* may be related to the fact that the free edge of the collar is interrupted in a similar position in *Cephalodiscus*. It may be noted, in this connexion, that SCHULTZ (**03**, 1, p. 405), in describing the regeneration of the lophophore in *Phoronis*, calls attention to a bifid condition of that structure which he specially compares with the two lophophoral arms of *Rhabdopleura*.

DE SELYS LONGCHAMPS (**04**, p. 38) gives a description of the vascular system of *Phoronis* differing in certain respects from that of most of his predecessors. It appears from his statements, confirming an earlier account by SCHNEIDER, that both the principal longitudinal vessels of the adult are differentiated on the dorsal side of the stomach of the larva, from a space which originates between the splanchnic mesoblast and the epithelium of the stomach, and (pp. 89—91) that they communicate with one another merely through a splanchnic sinus which has the same relations. It is perhaps significant, in this connexion, that the largest vessel in *Cephalodiscus* is the dorsal vessel (figs. 22, 33, 37; *d.v.*); that this vessel appears to originate from the wall of the stomach as a space between the splanchnic mesoderm and the digestive epithelium (figs. 57, 58); and that the only communication between the dorsal vessel and the posterior vessel of the stalk seems to be through a splanchnic or gastric sinus similar to that of *Phoronis*.

In his account of the muscular system DE SELYS LONGCHAMPS (**04**, pp. 108, 115) discusses the supposed predominance of that of the protocoele or proboscis-cavity in MASTERMAN's group Archichorda, and he comes to the conclusion that *Phoronis* does not shew this predominance. I may be permitted to point out that *Cephalodiscus* shews it no more than does *Phoronis*. The principal musculature of the former is assuredly the great mass of muscles in the stalk and on the antero-ventral side of the metasome. This is equally the case in *Phoronis*, in which (p. 115) "le tronc est la région musculaire par excellence".

With regard to the nervous system, and leaving on one side the description, which has not been confirmed by later authors, given by MASTERMAN (**97**, 1) of the peripheral nervous system of Actinotrocha, it may be noted that the nervous system of *Phoronis* remains in the epidermis, externally to the basement-membrane, and that there is evidence (DE SELYS LONGCHAMPS,

04, p. 97) of a general nerve-plexus in the epidermis of the entire lophophoral region. SCHULTZ **03**, 1, p. 406) finds that in regenerating specimens of *Phoronis* the central nervous system develops on the oral side of a dorsal invagination, which he compares with the medullary plate of Vertebrates and with the dorsal centre found in the collar of Balanoglossus. In his second paper (**03**, 2, p. 477) he confirms this homology, with the modification that he regards the invaginated ganglion as an adult organ which replaces the original larval ganglion, stating that a process takes place in Actinotrocha, at the time of metamorphosis, identical with what he describes in the regenerating *Phoronis*.

I formerly called attention (**87**, p. 46) to the resemblance between the ovarian mesenteries of *Cephalodiscus* and the lateral mesenteries of *Phoronis*, although suggesting that it was by no means certain whether the oviducts could be regarded as the representatives of the nephridia of *Phoronis*. MASTERMAN (**98**, 2, p. 512) has accepted this homology of the oviducts of *Cephalodiscus*. The consideration of the lateral mesenteries of *Phoronis* is, however, complicated by the difference of opinion which exists as to the interpretation which should be given to the mesentery which connects the oesophageal with the intestinal limb of the alimentary canal for some distance below the region of the nephridia. It has been maintained that this is a remnant of a dorsal mesentery, while it was suggested by CALDWELL (**82**, p. 373) that it is due to the secondary connexion of the intestine with the left lateral mesentery, which, nearer the lophophore, resembles the corresponding right mesentery in passing from the oesophageal limb to the body-wall (cf. CALDWELL's diagram, p. 383). The question has recently been discussed by DE SELYS LONGCHAMPS (**03**, p. 18), who accepts CALDWELL's view, pointing out that in Actinotrocha there is no trace of a dorsal mesentery, and (p. 22) that the lateral mesenteries are suspensory bands of the nephridia.

In *Cephalodiscus* the lateral mesenteries are suspensory mesenteries of the oviducts, but one of their principal functions is to carry the ovarian vessels originating from the dorsal vessel, which is contained in a dorsal mesentery. At their extreme dorsal end (figs. 149—152) they are connected with the body-wall of the metasome. They do not, however, originate from the pharyngeal limb of the alimentary canal, but from the dorsal mesentery and dorsal vessel. In view of the absence of the dorsal mesentery in Actinotrocha, this difference is perhaps not fundamental. The question of their homology in *Cephalodiscus* and *Phoronis* appears to me to turn on the propriety of regarding the oviducts of the former as comparable with the nephridia of the latter. The resemblance in the position of the external apertures of the two sets of organs is undoubtedly striking, and the organs are definitely compared with one another in two diagrammatic figures given by MASTERMAN (**98**, 2, figs. 16, 17). But the homology does not seem to me to be definitely established, and on the contrary it must be remembered that the genital ducts of Balanoglossus do not resemble nephridia.

M'INTOSH (**88**, p. 5) states that the "hyaline and often semi-translucent tube" of *Phoronis buskii* "is finely and concentrically striated, — layer upon layer of the hypodermic secretion entering into its composition"; and further that it includes "many minute sponge-spicules, diatoms, fragments of silex or accumulations of coarser sand-grains". It may be enquired whether there is any relation between the constitution of the tubes of *Phoronis* and that of the coenoecium

of *Cephalodiscus*; although if any such relation did exist it could hardly mean more than that the faculty of secreting a tube was formerly possessed by the epidermis generally. It may be noted that in Balanoglossus a "tenacious tube" is formed by mucus secreted by the epidermis, and that the surface of the proboscis and of the collar at least are concerned in the secretion of this tube (Morgan, **94**, pp. 17, 19).

In the budding processes of *Cephalodiscus* the coelomic cavities are almost certainly formed by the segmentation of a space derived from the virtual metasomatic cavity of the stalk. In *Phoronis* Schultz (**03**, 1, p. 409; 2, p. 487) states that the cavity of the lophophore, the supposed collar-cavity, is an outgrowth of the metasomatic coelom, both in normally developing larvae and in adults and larvae which are regenerating after artificial section.

One of the most striking features in which *Cephalodiscus* differs from Balanoglossus is the approximation of the anus to the mouth; and it can hardly be doubted that in *Cephalodiscus* and *Phoronis* the short line between the mouth and anus represents the dorsal surface. It is not impossible that the adult relations found in *Cephalodiscus* may be the result of ontogenetic processes similar to those which occur in the metamorphosing Actinotrocha. It is unfortunate that the study of the embryos found in the coenoecium has thrown no light on this point; but on the contrary the buds of *C. dodecalophus* (Pl. XIII, fig. 181) may give some clue to the manner in which the flexure of the alimentary canal has arisen.

In conclusion I may express the opinion that while *Phoronis* is not closely related to the Pterobranchia, its affinities are really in that direction; and that conclusion I have tentatively adopted in my article "Hemichordata" in Vol. VII of the 'Cambridge Natural History' (**04**).

(IV) Relations to other animals.

It would be going too far afield to discuss all the possible relationships of *Cephalodiscus*; and for a general consideration of this question I must content myself with referring to the works of Schimkéwitsch (**93**), Masterman (**96**, 1, 2; **98**, 1) and Delage and Hérouard (**97**, **98**).

Masterman (**96**, 1) has instituted a group Trimetamera, which includes the Hemichordata, the Echinodermata, the Brachiopoda, the Chaetognatha, the unarmed Gephyrea (with *Phoronis*), the Polyzoa and possibly the Mollusca, while he assumes that the Chordata diverged from the ancestral line which culminated in the Hemichordata. Schimkéwitsch (**93**) had previously expressed the same idea with regard to all these groups except the Mollusca, but he did not suggest any name for the assemblage.

If *Phoronis* be related to *Cephalodiscus*, the question naturally arises whether the Sipunculoid Gephyrea have affinities in the same direction. I may here refer to a paper by Shipley (**90**), who gives a diagram (fig. 32) of the lophophore of *Physcosoma* which is strikingly similar to my own diagram (Pl. XII, fig. 159) of *Cephalodiscus*. The lophophore of *Physcosoma* consists of a crescent, placed on the dorsal side of the mouth, with its concavity facing the anus. It bears a small number of short tentacles, which are provided, as in *Cephalodiscus*, with ciliated grooves on the sides corresponding with the outer or convex side of the crescent. Its dorsal ends are connected with a crescentic lower lip in precisely the same way as that in which the arms of *Cephalodiscus* join the operculum. The so-called "vascular system" is a closed space

surrounding the mouth and following the bases of the lophophore and lower lip; or, in other words, having the form of two crescents facing in the same direction and united at their tips. This double crescent extends into the lower lip, and sends off branches into the tentacles; and SHIPLEY suggests that it may be homologous with the "anterior body-cavity" of *Phoronis*; that is, with the praeseptal space which perhaps represents the collar-cavity. If there is anything in this suggestion, and if the arrangement has any relation to what is found in the Hemichordata, it is necessary to suppose that the proboscis has been greatly reduced — if it be not altogether absent — in *Physcosoma* as in *Phoronis*.

On the other hand GEROULD [1]) considers that the transitory metamerism which he has observed in the larva of *Phascolosoma*, together with other features, "indicate the close relationship between the Sipunculids and the Annelids". It appears however, from an earlier part of the same preliminary note that the metamerism consists of a division into four segments, noticed in the nerve-cord and in the mesoblastic bands immediately before the metamorphosis. This question of metamerism in Sipunculids is clearly one of great importance, but the small number of metameres mentioned by GEROULD suggests the possibility that the arrangement is not fundamentally different from that found in the Hemichordata.

Here, as in the case of the Brachiopoda, which are next considered, it appears to me that affinities to the Hemichordata may perhaps exist, but that the present state of our knowledge does not justify any positive statement on the subject.

The affinity of the Brachiopoda to the Hemichordata has been maintained by MASTERMAN (**98**, 1); while it was suggested some years earlier by CALDWELL (**83**) that these animals are related to *Phoronis*. In this connexion reference may be made to a recent embryological paper by CONKLIN [2]), who comes to the conclusion (p. 69) that "the affinities of *Phoronis* and Brachiopoda are well established", and (p. 70) that except for the absence of segmentation in the coelom, "there are no important differences between Actinotrocha and the brachiopod larva".

The account given by CONKLIN is a confirmation of the general accuracy of the figures published by KOWALEVSKY in 1874. The development of the Brachiopoda, as indicated by these two observers, shews certain resemblances to that of the Enteropneusta and of *Cephalodiscus*. There is, for instance, a conspicuous anterior region of the body-cavity which is developed as an unpaired enterocoel from the front of the archenteron. The mantle-fold of the young larva forms a more or less equatorial swelling, which gives rise to the appearance of a division of the entire larva into three segments. MASTERMAN (**98**, 1, p. 288) gives a figure indicating that the second of these "segments" (the mantle-fold) is the equivalent of the collar of the Enteropneusta, although he explains on the preceding page that the arms as well as the mantle are to be regarded as derivatives of this region. From the account which has recently been given by YATSU [3]) of the development of *Lingula*, it would, however, appear that the arms develop from a region which is in front of that of the mantle-fold; and it is not easy to assume that both

1) J. H. GEROULD, "The Development of *Phascolosoma*", Arch. Zool. Exp. et Gén. (4) II, Notes et Revue, 1904, N° 2, p. XVII.
2) E. G. CONKLIN, "The Embryology of a Brachiopod, *Terebratulina septentrionalis*"; Proc. Amer. Phil. Soc. XLI, 1902, p. 41.
3) N. YATSU, "On the Development of *Lingula anatina*", Journ. Coll. Sci. Tokyo, XVII, 1901—1903, Art. 4.

the arms and the mantle belong to the collar. Now those zoologists who have supported the view that the Brachiopoda are related to *Phoronis* and to other tentaculiferous animals have assumed that the lophophores are homologous structures in the several groups. If then the arms are to be regarded as the representatives of those of *Phoronis* or *Cephalodiscus*, it seems to follow from the evidence of *Lingula* that the mantle-fold is not part of the collar; — or, in other words, that the structure which in the larvae of certain Brachiopods appears to represent the collar is not in reality of that nature. I do not in fact find much in YATSU's account which obviously confirms the view that the Brachiopoda are related to the Hemichordata.

It must, however, be noted that BLOCHMANN [1]), as the result of his careful studies on the anatomy ot Brachiopoda, is convinced of the affinity of this group to *Phoronis*, the Sipunculids and the Polyzoa. The relationship is nearest between Brachiopods and *Phoronis*, with which the Sipunculids are connected; while the affinities to the Polyzoa are more remote.

I do not feel myself qualified to criticize the view of the Brachiopod affinities of the Hemichordata, particularly in the absence of information with regard to many features of importance in the later development of the Brachiopoda. But the testimony of such authorities as BLOCHMANN cannot be ignored; and if this observer is right in maintaining that the Brachiopoda are related to *Phoronis*, it may perhaps follow that they are also related to *Cephalodiscus*.

Although it appears to me probable that the Hemichordata are related both to the Echinodermata and to the Chordata, I do not propose to discuss these questions at length, since their consideration is more easily approached from the side of Balanoglossus than from that of *Cephalodiscus*. Independently of the papers dealing with the resemblances of Tornaria to Echinoderm larvae, the affinity between the Enteropneusta and the Echinodermata has been maintained by BURY (**88**, p. 295; **95**, p. 125), MACBRIDE (**96**, p. 395), MASTERMAN (**98**, 1, p. 289; **02**, p. 403) and others, and it is recognised as possible by SPENGEL (**93**, p. 750).

The question of the Chordate affinities of the Hemichordata has formed the subject of numerous papers. As long ago as 1877 HUXLEY (**77**, p. 674) went so far as to institute a group Pharyngopneusta for the reception of the Enteropneusta + Tunicata, in allusion to the existence of gill-slits in both groups. The affinity is rejected by SPENGEL (**93**, p. 721), but it is supported by BATESON (**86**), MASTERMAN, MACBRIDE (**98**, **00**), WILLEY (**94**; **99**, 2, p. 295) and others. KEMNA (**04**, pp. 50, 52) considers that *Cephalodiscus* more nearly resembles the common ancestor of the Chordata than does any other living form. Although I do not discuss the views of these writers, the important recent work by VAN WIJHE (**01**) on the head of Amphioxus seems to me to call for special remark.

VAN WIJHE accepts, though with some modifications, MACBRIDE's account (**98**, **00**) of the development of the coelomic cavities of Amphioxus, according to which the embryo is constructed on the Hemichordate type so far as it possesses representatives of the protocoel, the mesocoels and the metacoels.

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1) F. BLOCHMANN. — "Über die Anatomie und die verwandtschaftlichen Beziehungen der Brachiopoden", Arch. d. Ver. d. Freunde d. Natg. Mecklenburg, Jg. 46, 1892, p. 37.

The cavities in the head of the adult are very complicated; and, if I have understood the original account correctly, they may be described as follows. —

(I) a system of "Schnauzenhöhlen" in contact with the anterior end of the notochord. Of these, which I may allude to as the praeoral cavities, there are four; two lying respectively along the dorsal and ventral sides of the notochord, and the other two having a lateral position.

(II) the "Stomocoel", composed of right and left halves, which are very unequally developed. The ventral mesentery which separates the two cavities lies at the right side of the mouth, which is thus, in the adult as in the larva, an organ of the left side. The right stomocoel (loc. cit., fig. 23) has a dorso-ventral portion at the side of the true mouth, prolonged forwards as a longitudinal tube which lies on the right side of the roof of the buccal cavity. Ventrally the stomocoel passes into the right "epipterygial cavity", which lies on the ventral side of the mouth and of the beginning of the pharynx, dorsally to the pterygial or sub-atrial muscles. The left stomocoel is much more complicated. Its large epipterygial portion is separated from the corresponding right cavity by a well developed ventral mesentery, the asymmetrical position of which has already been noticed. The "outer lip-cavity" is a direct anterior continuation of the left epipterygial cavity, and it occupies the outer or ventral portion of the lip, which itself forms the floor of the (praeoral) buccal cavity; sending a prolongation into each of the oral cirri. The "inner lip-cavity" occupies the whole of the dorsal side of the lip, and is therefore close to the buccal cavity. It is said to be in origin a part of the left stomocoel. The "velicavum", or coelom of the velum, is continuous with the left stomocoel in the larva, but in the adult it resembles the inner lip-cavity in being completely closed. It is regarded as the left antimere corresponding with the dorso-ventral portion of the right stomocoel, altered in position owing to the assumption of a transverse position by the mouth, which in the larva opens on the left side. Each epipterygial cavity is continuous with the "pterygocoel" or "Seitenflossenhöhle" of its own side, a space which is better known under the name of the metapleural or lymph-canal.

(III) the "peribranchial cavity", consisting of the two dorsal spaces at the sides of the hyper-pharyngeal groove, the unpaired ventral portion which underlies the endostyle, and the coelomic spaces of the pharyngeal bars which connect the dorsal and ventral parts. The coelom of the first pharyngeal bar differs from the similar spaces in the other bars by running from the epipterygial cavities to the ventral or endostylar coelom of the pharynx.

The comparison made by VAN WIJHE with the Enteropneusta gives the following results. The dorsal praeoral cavity is not accounted for. The ventral cavity constitutes the whole of the anterior body-cavity, since VAN WIJHE holds that the left head-cavity of other authors is not part of the protocoel, but on the contrary is derived from ectoderm. The left "head-cavity" gives rise, as is well known, to the "Räderorgan", or system of ciliated grooves of the buccal cavity; and it is regarded as the representative of the stomodaeum of Craniata, and of the dorsal tubercle of Ascidians. "HATSCHEK's groove", which is an anterior prolongation of the Räderorgan, represents the subneural gland of Ascidians and the notochord of Hemichordata.

The lateral praeoral cavities are derived from the collar-cavities, and are in fact the antero-dorsal processes shewn in HATSCHEK's well known figs. 50—52 (**81**) of an embryo of Amphioxus. The remainder of the collar-cavities is constituted by the right and left stomocoels, together with at least three myotomes (p. 68), and the anterior parts of the metapleural canals. These had been supposed by MACBRIDE, in his earlier paper (**98**), to belong entirely to the collar, but VAN WIJHE considers that their innervation shews that they belong for the most part to the metasome, only their anterior ends belonging to the collar. The collar thus ends, as in Enteropneusta, at the beginning of the branchial region, and the more posteriorly situated coelomic spaces belong to the metasome, which by a secondary segmentation has given rise to the remainder of the myotomes. The collar-canals of the Hemichordata are represented in Amphioxus by the first pair of nephridial tubules, which open from the epipterygial cavities (= parts of the collar-cavities) into the atrium.

VAN WIJHE thus definitely recognises the affinity of the Hemichordata to Amphioxus. The latter is indeed placed, with the Tunicata and the Craniata ("Craniota") in the Chordata; while the Enteropneusta and *Cephalodiscus*, constituting the Pharyngotremata, are associated, with *Rhabdopleura* and *Phoronis* (to which no group-name is assigned) as Prochordata. But he carries the comparison even further than has been done by most morphologists, since he considers (p. 69) that the protocoel, mesocoels and metacoels can be identified in the embryos of *Petromyzon*, Elasmobranchs and even in the higher Craniata, while (p. 70 n.) a proboscis-pore can be recognised in the embryos of Elasmobranchs.

It appears to me that a critical examination of VAN WIJHE's views can only be made as the result of an independent investigation of Amphioxus; but there are nevertheless one or two points on which I should like to comment. The account of the collar-cavities is undoubtedly of interest, confirming as it does the general accuracy of MACBRIDE's observations on the development of Amphioxus. Fig. 27, 28, and 32, given by VAN WIJHE, are specially significant in shewing the existence, in the adult Amphioxus, of a well marked transverse septum between the collar-cavities and those of the metasome. The prolongation of the outer lip-cavity into the oral cirri may indicate that the floor of the buccal cavity corresponds with part of the operculum in *Cephalodiscus*, while somewhat further back the collar-cavity is subdivided by a ventral mesentery (cf. figs. 9—18), as in the same animal. The backward extension of this region of the collar, on the ventral side of the pharynx, is also suggestive. Thus VAN WIJHE's fig. 15 represents an arrangement which is similar to what may be seen in sections of *Cephalodiscus* transverse to the long axis of the zooid, in which the metasomatic cavities occupy the dorsal part of the section, while the collar-cavities still appear on the ventral side, subdivided by a median mesentery. Taking this into consideration with HATSCHEK's figs. 50—52 (**81**) of an embryo, there is a remarkable similarity between the collar-cavities of *Cephalodiscus* and Amphioxus, the coelomic sac in both cases having a triangular form when seen from the side, the dorsal part being much longer than the ventral part. While in *Cephalodiscus* the elongated dorsal region of the collar-cavity is connected with the arms, the anterior parts of the same region in Amphioxus are cut off to form the lateral praeoral cavities ("Schnauzenhöhlen") of VAN WIJHE. The relations of the collar-cavities of the larval Amphioxus to the notochord and to the ventral

praeoral cavity, as shewn in HATSCHEK's fig. 145, suggest that the ventral cavity may correspond with that part of the anterior body-cavity of *Cephalodiscus* which lies in the proboscis-stalk, ventrally to the notochord; and that in fact the proboscis in Amphioxus is represented only by a part of the proboscis-stalk. It would be interesting to know more of the nature of VAN WIJHE's dorsal praeoral cavity ("Schnauzenhöhle"); and it is conceivable that it might be the homologue of the pericardium of the Enteropneusta.

The only group with regard to which it appears necessary to say more is that of the Polyzoa. A large number of writers have assumed — and it appears to me on inadequate grounds — that *Phoronis* is related to the Polyzoa. If *Phoronis* be so related, it is not foreign to the object of this memoir to consider the question in its bearings on *Cephalodiscus*.

It may be remembered at the outset that on the occasion of the first discovery of *Rhabdopleura* by SARS and NORMAN, no doubt was entertained of the correctness of the view that this animal was an aberrant Polyzoon. The later discovery of *Cephalodiscus*, and its association with *Rhabdopleura*, naturally led to the same view being adopted with regard to the subject of this Report. With the discovery that *Cephalodiscus* has affinities in the direction of Balanoglossus, it appeared reasonable to remove it from the Polyzoa, since these animals had not been shewn to possess any of the characters which specially connect *Cephalodiscus* with Balanoglossus. What holds good for *Cephalodiscus* must, I think, also apply to *Rhabdopleura*.

In again taking up the study of *Cephalodiscus* I have seen no sufficient reason for modifying the views I formerly expressed (**87**) with regard to this question. It might indeed be maintained that the embryo of *C. gracilis* with its large internal yolk-mass, its conspicuous ventral invagination of ectoderm and its "pyriform organ" was directly comparable with the larva of one of the marine Ectoproctous Polyzoa. To this might perhaps be added the fact (if it be a fact) that in both groups the alimentary canal of the bud is developed entirely from an invagination of the outer layer.

It remains to be seen whether the later developmental history of *Cephalodiscus* will throw any further light on this particular question; but for my own part I do not anticipate that it will tend to strengthen the view that the Pterobranchia are allied to the Polyzoa. In order to accept this view it is necessary either to regard the Ectoprocta as the most primitive of the Polyzoa, or to take the view — which is adopted by KORSCHELT and HEIDER in their well known text-book of Embryology — that the Ectoprocta have no close affinity to the Entoprocta. It appears to me that this view is untenable, and I may fortify my own opinion by quoting that of PROUHO [1]), the excellence of whose work in both subdivisions entitles him to speak with authority, that "Aujourd'hui, aucun des zoologistes qui étudient les Bryozoaires ne met en doubte "le bien fondé des vues de Nitsche" [to the effect that the Entoprocta and the Ectoprocta are two groups belonging to the same phylum]. The Entoprocta, on this view, furnish many clues to the understanding of the Ectoprocta. In particular, the comparative study of the development, taking into account such questions as the structure of the larvae of Entoprocta, the metamorphosis of *Pedicellina*, and the structure of *Cyphonautes* appears to me to shew that the Polyzoa, as

1) H. PROUHO, "Contribution à l'Histoire des Bryozoaires", Arch. Zool. Exp. et Gén. (2) X, 1892, p. 641.

the term is usually understood, are a monophyletic group, and that the larval forms of the Ectoprocta receive a reasonable amount of explanation by comparing them with the larvae of Entoprocta. The attempt to explain the facts in the converse direction has, I think, never been seriously attempted; nor can I believe that it would be successful, particularly if the Phylactolaemata were taken as the starting point. It must be remembered that the Phylactolaemata are the forms which have most frequently been compared with *Phoronis*.

Another fact of which sufficient account is not usually taken in comparing *Phoronis* with the Polyzoa is the palaeontological evidence. The Polyzoa are a very ancient group, and the earliest known forms do not appear, so far as can be judged from their calcareous skeletons, to shew any approach to *Phoronis* or to *Cephalodiscus* or to any form which might fairly be supposed to have been ancestral to either of these.

I do not feel myself competent to express any opinion with regard to the view adopted by SCHEPOTIEFF (**04**, p. 17) that *Rhabdopleura* is related to the Graptolites.

In conclusion, I may state my opinion that while *Rhabdopleura* is the nearest living ally of *Cephalodiscus*, the affinity of both these genera to the Enteropneusta has been clearly demonstrated. I am inclined to accept the view that they have affinities in the direction of *Phoronis*, the Chordata and the Echinodermata, and to reject the suggestion that they are in any way related to the Polyzoa.

XIX. *RHABDOPLEURA*.

While this Report was going through the press Professor WEBER sent me a stone from Station 204 in the hope that it might bear additional specimens of *Cephalodiscus sibogae*. No such specimens were found, but a microscopical examination of the surface of the stone was rewarded by the discovery of a colony of *Rhabdopleura*. Although the specimen is a mere fragment, with its zooids in poor condition, its occurrence in the "Siboga" dredgings is of considerable interest in extending the geographical range of *Rhabdopleura*, which is indeed probably world-wide in its distribution. Originally known from deep water off Shetland and the Norwegian coasts, by the labours of NORMAN, ALLMAN and G. O. SARS, and more recently described from one of the same districts by LANKESTER and SCHEPOTIEFF, it has since been recorded from the coasts of Ireland and Brittany, by HINCKS and JULLIEN respectively; from Tristan d'Acunha in the South Atlantic by FOWLER; and from the Azores by JULLIEN; while its extreme recorded limits are West Greenland [1]) and South Australia (HARMER, **04**, p. 23).

Several species of *Rhabdopleura* have been described, although in the absence of a comparative study of the genus it is uncertain how far these are really distinct. The specimens from the North Sea, from Greenland and from Tristan d'Acunha are described as *R. normani* Allman (= *R. mirabilis* Sars). Those from Ireland and Brittany are known as *R. compacta* Hincks;

1) NORMAN, Ann. Mag. Nat. Hist. (7) XII, 1903, p. 101 n.

while the specimens from the Azores are said to belong to two species, *R. grimaldii* Jullien, and *R. manubialis* Jullien.

R. normani appears to be characterised by the great length of the peristomes, or free cylindrical parts of the tube. *R. compacta* is said to have very short, crowded peristomes. *R. grimaldii* has a short peristome, continuing a creeping portion of equal length, which is characterised by the presence of "deux tubes très fins, convergeant par leur extrémité antérieure", and running longitudinally along its free wall; while the orifice is somewhat expanded. In *R. manubialis* the peristome is about twice as long as the attached portion of the zooecium, and its tube-rings seem to be very prominent. The species is not, however, very well characterised, although it is said to differ from *R. grimaldii* by the colour of the coenoecium (yellowish instead of brown), by the absence of the two "tubes" of that species, and by the fact that the axial cord or pectocaulus extends into the attached part of the zooecium, which is not the case in *R. grimaldii*.

The specimen dredged by the "Siboga" is a perfectly typical *Rhabdopleura*, its coenoecium consisting of a creeping portion attached to the stone, and provided with the characteristic, dark brown pectocaulus embedded in its lower wall.

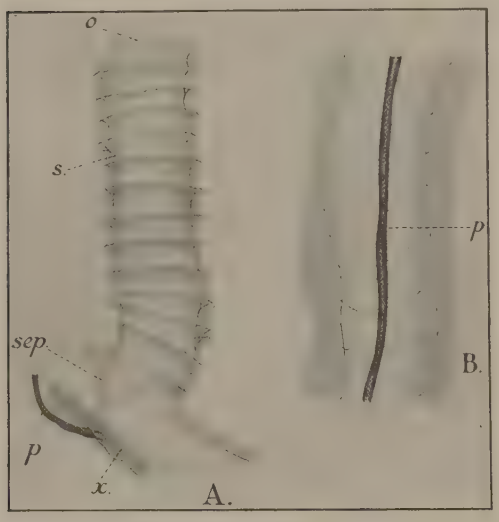

Fig. 2. — *Rhabdopleura* sp. (Stat. 204). *A*, a complete peristome, originating from part of the creeping portion of the coenoecium; *B*, fragment of the creeping portion: *o.*, orifice; *p.*, pectocaulus; *s.*, suture of tube-ring; *sep.*, septum; *x.*, mass of detritus (× 80: magnified to the same extent as the free end of the peristome of *R. normani* shewn in Pl. II, fig. 19).

I have been able to examine only two peristomes which appear to be complete. The specimen figured (*A*) consists of 13 rings, the last of which seems to have been somewhat distorted during the preparation of the slide. The rings are much more prominent than in *R. normani*, giving the peristome an annulated appearance. As in that species the substance of the ring is not completely continuous, but is interrupted by a suture (*s.*), which is visible, however, only in cases in which it happens to occupy a favourable position. In the creeping portion of the zooecium (*B*), the sutures have the characteristic zigzag disposition which has been noticed in other species of *Rhabdopleura*. The junctions of successive lamellae in this portion form ridges which, however, are not so prominent as those of the peristomes. The creeping part is interrupted by transverse septa (*A*, *sep.*), as in other species of the genus, and its lower or attached wall contains the tubular pectocaulus (*p.*). The preparation shews one zooid, with recognisable tentacles, and indications of several buds [1]).

1) The stone on which the *Rhabdopleura* was found bore several tubes which in size and in being composed of a series of distinct rings have a curious resemblance to the peristomes of *Rhabdopleura*. One or two of these structures were in fact mounted under the impression that they belonged to that genus. Their wall is, however, much thinner than in *Rhabdopleura*, the rings are made up of a series of smaller segments, and the tubes are conical instead of being cylindrical in form. There can be no question that they belong to *Stephanoscyphus*, and I am unable to distinguish them from *S. mirabilis* described by Allman in 1875 (Trans. Linn. Soc., (2), Zool., I, p. 61). Professor Ch. Julin, to whom I sent a preparation of the organism, informs me that he agrees with this determination.

My examination of *Cephalodiscus* has convinced me that the characters of the coenoecium form a reliable means of distinguishing the species in that genus. I am accordingly inclined to think that the specimen of *Rhabdopleura* from Station 204 is probably a new species, characterised by the small number of tube-rings, by their comparative delicacy and thinness, and by their angular projection to the exterior. The specimen is, however, so fragmentary that I do not consider myself justified in giving it a specific name. It may be hoped that other specimens will hereafter be found among the "Siboga" dredgings which will make it possible to come to a more satisfactory conclusion on this point. There is at present no reason for assuming that the peristomes found have acquired their full number of rings.

The following comparison of the "Siboga" specimen with Norwegian specimens of *R. normani* illustrates some of the differences between the two forms: —

	Rhabdopleura sp. ("Siboga")	*R. normani.*
Number of rings of peristome	13—15	50—60
Length of peristome	·64—·70 mm.	2·59—2·88 mm.
Diameter of peristome	175—210 μ.	255—270 μ.
Thickness of wall of peristome, at the middle of a tube-ring.	7·5—11·5 μ.	16—24 μ.
Diameter of pectocaulus	20—22 μ.	32 μ.

It will be observed that the East Indian form is in all respects smaller than the Norwegian form, while the thickness of the wall of its peristome is distinctly less.

The following synonymy gives references to some of the more important memoirs dealing with *Rhabdopleura*. Other papers, not mentioned here, are referred to by FOWLER (**92**, 2).

R. normani Allman.

R. normani Allman, (Quart. J. Micr. Sci. IX, 1869, p. 58; Rep. Brit. Ass. (Norwich meeting, 1868), 1869, p. 311; HINCKS (**80**), p. 580, Pl. LXXXII, figs. 1, 2, 4—7; LANKESTER (**84**), p. 622, Pls. XXXVII*bis*—XLI; FOWLER (**92**, 1; **92**, 2; **04**); NORMAN, Ann. Mag. Nat. Hist. (6) XIII, 1894, p. 131; (7) XII, 1903, p. 101 n.; CONTE et VANEY (**02**, 1, 2); SCHEPOTIEFF (**04**).
R. mirabilis Sars (**72**); Quart. J. Micr. Sci. XIV, 1874, p. 23.

R. compacta Hincks.

R. compacta Hincks (**80**), p. 581, Pl. LXXII, figs. 8, 8*a*, 9; JULLIEN, Bull. Soc. Zool. France, XV, 1890, p. 183.

R. grimaldii Jullien.

R. grimaldii Jullien, Bull. Soc. Zool. France, XV, 1890, p. 180; JULLIEN et CALVET (**03**), p. 23, Pl. I, figs. 1*a*, 1*b*.

R. manubialis Jullien.

R. manubialis Jullien et Calvet (**03**), p. 24, Pl. I, fig. 2.

S. mirabilis appears to be identical with *Spongicola fistularis*, described by F. E. SCHULZE in 1877, and it has been demonstrated by the observations of S. LO BIANCO and P. MAYER (Zool. Anz., XIII, 1890, p. 687; cf. also MELLY, Rep. Brit. Ass. (Cardiff, 1891), 1892, p. 368) that this is the Scyphistoma form of *Nausithoë*. Two other species of *Stephanoscyphus* are described by KIRKPATRICK (Ann. Mag. Nat. Hist. (6), V, p. 13), one of them from the China Sea. *Nausithoë* is recorded by MAAS in his account of the Scyphomedusae collected by the "Siboga"-Expedition (Monogr. XI, 1903, p. 19).

Rhabdopleura normani has already been referred to in this Report on p. 8 (coenoecium), on pp. 52, 78 (stalk), on pp. 81, 87 (reproductive organs), and on p. 92 (budding). Should the genus include more than one species it may, however, be questioned whether the form described by FOWLER from Tristan d'Acunha is really identical with *R. normani*.

XX. SUMMARY OF THE PRINCIPAL RESULTS.

(1). The geographical and bathymetrical range of *Cephalodiscus* are largely extended by the description of three new species from Oriental waters, one of them (*C. gracilis*) having been obtained, at or near low tide mark, on a Coral Reef on the coast of Borneo. The second (*C. sibogae*) is from 75—94 metres off the S.E. point of Celebes, while the third (*C. levinseni*) is from about 183 metres at the S. end of the Corea Strait.

(2). While the specimens of *C. gracilis* and *C. levinseni* resemble the "Challenger" specimens of the type-species (*C. dodecalophus*) in consisting exclusively of female individuals, that of *C. sibogae* is of the male sex. The possibility is not excluded that *C. sibogae* may be the male of *C. gracilis*; but it is concluded that it is really a distinct species.

(3). The colony of *C. sibogae* offers a striking case of dimorphic zooids. Certain individuals are of the type characteristic of a female *Cephalodiscus* except for the absence of gonads. These are termed neuters, and they doubtless provide for the nutrition of the colony. The remaining individuals are males, and are remarkable for the vestigial nature of the apparatus connected with the collection and digestion of food. Their curiously modified arms are reduced to a single pair, which are not provided with tentacles; the operculum is absent; and the alimentary canal is in a vestigial condition. The principal organs are a pair of large testes, which correspond in the position of their external apertures and in their relation to the dorsal vessel with the ovaries of the females of other species. The proboscis is well developed, while the central nervous system, the body-cavities, the collar-canals and the vascular system resemble those of an ordinary *Cephalodiscus*. Their nutrition is probably provided for by vascular connexions with the neuter individuals.

(4). The characters of the coenoecium are shewn to be of importance in discriminating the species.

(5). The zooids of the several species, while differing from one another to a marked extent in form, in the number of their tentacular arms, and in the characters of their stalk, are strikingly uniform in all essential points of structure.

(6). The arms and operculum are regarded as modifications of the anterior free edge of the collar. The number of arms of the female or neuter zooids ranges from four pairs in *C. sibogae* to six pairs in *C. dodecalophus* and *C. levinseni*; *C. gracilis* occupying an intermediate position in possessing five pairs of arms.

(7). The structure of the collar-pores or collar-canals is described, and it is shewn that they are closely related with parts of the muscular system; suggesting that their modus operandi is partly due to muscular action.

(8). The stalk differs widely in proportions in the several species, and is specially long and slender in *C. gracilis* and in *C. sibogae*.

(9). The structure of the pharynx is described, and the probable mode of feeding is considered.

(10). The most important constituents of the vascular system are (*a*) a large dorsal vessel applied to the dorsal surface of the pharynx, and sending off vessels to the gonads; (*b*) the anterior and posterior vessels of the stalk. The anterior stalk-vessel is continuous with the corresponding vessel of the trunk. The posterior stalk-vessel ends on the wall of the second stomach, and is probably in communication with the dorsal vessel through a perigastric sinus.

(11). Some account is given of the early development, which appears to shew some resemblances to that of the large-yolked species of Balanoglossus. The five coelomic spaces of the adult can be recognised in the embryo. The latest embryos are not old enough to give any indication with regard to the mode in which most of the adult characters are acquired. The two species investigated (*C. gracilis* and *C. levinseni*) differ to a striking extent in some of their embryonic characters.

(12). A partial account is given of the budding, in *C. gracilis* and in *C. dodecalophus*. The position of the parts of the alimentary canal of the bud shews some approach to the condition found in Enteropneusta, the pharynx and stomach lying in the morphologically antero-posterior line.

(13). *Cephalodiscus* shews unmistakeable affinities to *Rhabdopleura* and to the Enteropneusta. It is probably related to *Phoronis*; and, through Balanoglossus, to the Echinodermata and the Chordata; but it is not nearly related to the Polyzoa.

[**Postscript.** — An interesting note by Schepotieff (**05**) on *Rhabdopleura* has appeared just as this sheet was about to be printed off. The paper contains important results with regard to the body-cavities, proboscis-pores, pleurochordal grooves, pericardium, vascular system, muscles, testis and budding, and it appears to me to complete the proof of the fundamental resemblance in structure between *Rhabdopleura* and *Cephalodiscus*. The extra-oral parts of Schepotieff's "Kiemenrinnen" are what I describe as the "food-channels" in this Report. The alimentary canal of the bud is developed partly from an endodermic "Anlage", and not as I suppose it to be developed in *Cephalodiscus*].

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EXPLANATION OF PLATES I XIV

The scale of the figures is indicated on each plate, and is further explained in the legend, in each case. The plane of the sections and the nomenclature of the surfaces are described in accordance with the text-figure on p. 23; a section transverse to the actual principal axis of the zooid being regarded as "frontal", while a "transverse" section is parallel to that plane. The terms "right" and "left" are used for descriptive purposes, and do not necessarily correspond with the actual right and left sides of the original specimens. Certain details are omitted in some of the figures: thus the nerve-layer of the epidermis is only shewn when it is unmistakeably present; while many of the strands which traverse the collar-cavities are omitted.

LIST OF REFERENCE-LETTERS.

a. arm.
a. b. arm-base.
al. alimentary canal.
an. anus.
a. v. anterior vessel of stalk.
a. v.' anterior vessel of body.
b. bud.
b. c.[1] proboscis-cavity.
b. c.[2] collar-cavity.
b. c.[2] *a.* anterior dorsal horn of collar-cavity.
b. c.[3] metasomatic cavity.
b. c.[3] *a.* anterior ventral horn of metasomatic cavity.
b. c.[3] *b.* part of metasomatic cavity in loop of alimentary canal.
b. m. basement-membrane.
b. w. body-wall.
c. collar.
c. c. collar-canal.
c. c. e. external opening of collar-canal.
c. c. i. internal opening of collar-canal.
c. n. s. central nervous system.
d. basal disc of stalk.
div. dorsal diverticulum of pharynx.
d. m.[2] dorsal mesentery of collar.
d. m.[3] dorsal mesentery of metasome.
d. v. dorsal vessel.
e. embryo.
ep. epidermis.
e. r. epithelial ridge.
exc. excretory granules.
f. fold of body-wall.
f. c. food-channel.
f. c. l. left food-channel.
f. c. r. right food-channel.
fil. peristomial filament.
g. gonad.
gl. glomerulus.
g. p. generative pore.
g. s. gill-slit.
g. s. e. external opening of gill-slit.
int. intestine.
L. 1—6. left arms.
L. a. left arm.
l. g. labial or oral groove.
l. n. lateral nerve.
m. mouth.
mes.[2] dorsal mesentery of collar.
mes.[3] dorsal mesentery of metasome.
met. metasome or trunk.
m. r. mid-rib of peristome.
ms. longitudinal muscles of metasome.
ms. p. muscles of proboscis.
nch. notochord.
n. t. nerve-tract.
o. orifice of coenoecium.
oes. oesophagus.
op. operculum.
op. l. left lobe of operculum.
op. r. right lobe of operculum.
op. rec. recess at base of operculum.
or. m. oral muscle (of collar).
or. s. oral sinus (?).
ov. ovary.
ovd. oviduct.
ov. l. left ovary.
ov. m. ovarian mesentery.
ov. r. right ovary.
ov. v. ovarian vessel.
p. proboscis.
p.' its ventral lobe.
p. b. pigment-band of proboscis.
per. pericardium.
per. s. pericardial sinus or heart.
ph. pharynx.
pl. g. pleurochordal groove.
post. p. posterior pit of embryo.

p. p. proboscis-pore.
pr. l. primary lamella of coenoecium.
prob. st. proboscis-stalk.
pst. peristome.
pt. peritoneum.
p. v. posterior vessel of stalk.
p. v.' its termination on the alimentary canal.
r. rectum.
R. 1—6. right arms.
R. a. right arm.
rec. recess into which oviduct opens.
s. $^1/_2$ septum between proboscis and collar.
s. $^2/_3$ septum between collar and metasome.
sec. l. secondary lamella of coenoecium.
s. o. sense-organ of embryo.
sp. mass of spermatozoa.
st. stalk.
stom. stomach.
stom.^{2} second stomach.
t. testis.
tent. tentacles.
t. l. left testis.
t. r. right testis.
t. v. vessel of testis.
u. l. upper lip.
vac. vacuolated ectoderm of embryo.
v. inv. ventral invagination of embryo.
v. m. vitelline membrane.
v. mes.^{2} ventral mesentery of collar.
v. mes.^{3} ventral mesentery of metasome.
v. t. ventral thickening of embryo.
x. problematical tissue of collar-canal.
y. thickening of ectoderm near anus.
yk. yolk.
yk. a. its anterior subdivision.
z. zooid.

PLATE I.

Figs. 1, 4, 7, 8, 9. — *Cephalodiscus gracilis.*
Figs. 2, 3. — *C. sibogae.*
Figs. 5, 6, 10. — *C. levinseni.*

Fig. 1. *C. gracilis*, × 1. — The left hand portion of the figure shews a portion of the colony, detached from the substratum; its transparent coenoecium containing masses of orange-coloured zooids. The right hand portion shews another part of the coenoecium, including but few zooids, growing on a species of *Tubucellaria* (probably *T. fusiformis* D'Orb.).

Fig. 2. *C. sibogae*, × 1. — Shewing the erect, orange-coloured tubes of the coenoecium, originating from a basal encrustation on a stone. The dark masses seen in the tubes to the left of the figure are zooids, most of which are, however, retracted into the basal encrustation, which owes its dark colour to the zooids contained therein. The colour of the stone has not been indicated.

Fig. 3. *C. sibogae.* — Anterior view of a neuter individual. Of the five arms seen on the right side of the drawing, the most posterior belongs to the right side, while the others are the four left arms. One of the right arms is marked *R. a.*, but the details cannot be made out in the preparation. The only part of the operculum which can be distinctly seen is that marked *op. l.*

Fig. 4. *C. gracilis.* — Group of buds. Two budding systems, marked respectively *A* and *B*, are intermingled: the numbering indicates the approximate relative ages of the individuals. The system *A* consists of four degenerated stalks (*A. 1—4*) and a single bud (*A. 5*), which has two arms (not drawn). The system *B* consists of a basal disc (*d.*), belonging to the degenerated stalk *B. 1*: *B. 2, 3* are degenerated stalks: *B. 4* shews five right arms and three left arms: *B. 5* is seen in anterior view, two arms (not shewn) being moderately well developed on its right side: *B. 6* has a single pair of arms, indicated as spherical knobs: *B. 7* has just differentiated its proboscis.

Fig. 5. *C. levinseni.* — Young zooid. The complicated fold of the anterior surface of the proboscis is represented with only partial success. The stalk (*st.*), which is much like that of *C. dodecalophus*, is overlapped by the proboscis: — *a*, mass of arms and tentacles.

Fig. 6. *C. levinseni.* — Side view of an older zooid. The proboscis is in the reversed position which it frequently assumes in this species, as is indicated by the position of the pigment-band (*p. b.*).

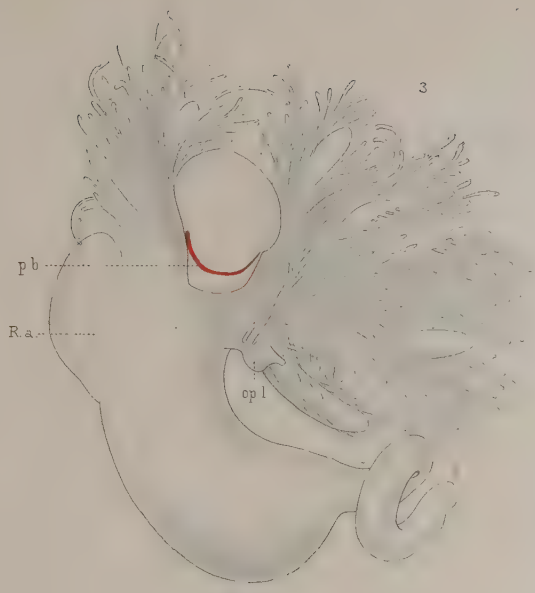
Fig. 7. *C. gracilis.* — Side view of adult zooid.

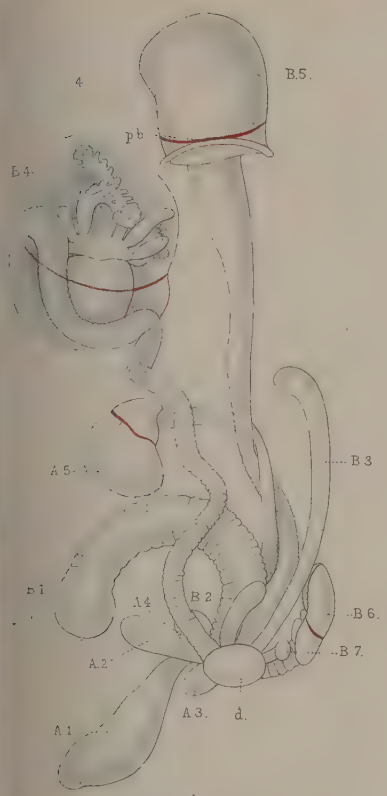
Fig. 8. *C. gracilis.* — Posterior view of a young bud with a single pair of arms (*a.*). The pigment-band of the proboscis is already developed, and is seen through the metasome (*met.*), while the collar (*c*) is marked off from the metasome by a slight dorsal groove.

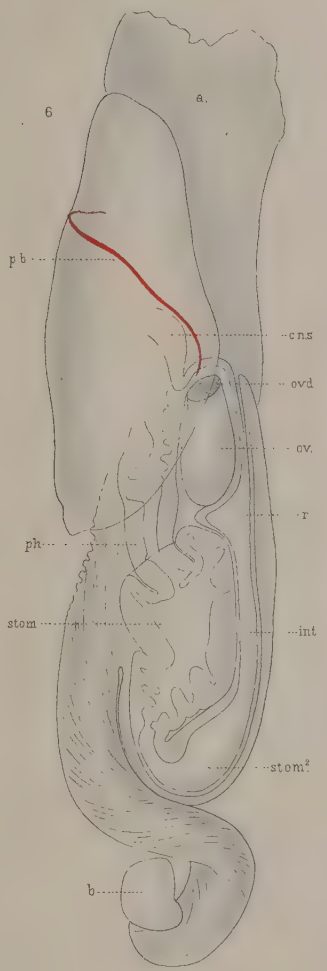
Fig. 9. *C. gracilis.* — Anterior view of an older bud, from the same budding system as fig. 8. The arms are seen through the proboscis. The young posterior arms are seen at the base of the two well developed arms on the left of the figure.

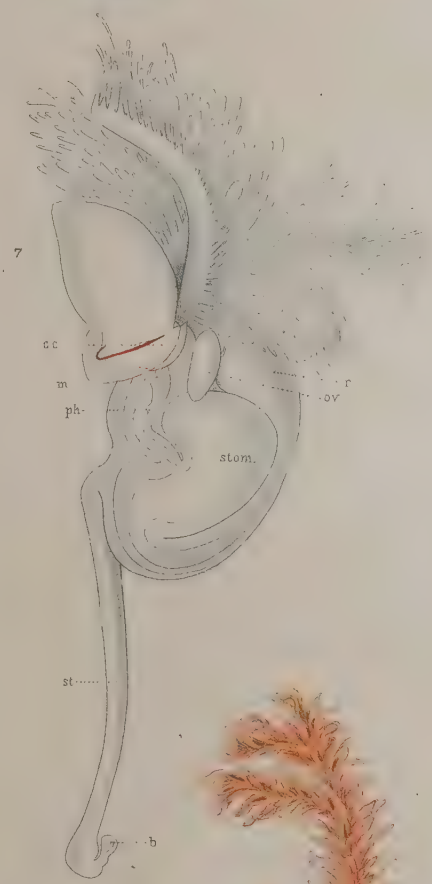
Fig. 10. *C. levinseni.* — Part of the coenoecium, × 1, represented in its natural colour. Some of the elongated zooids are visible in the cavities of the zooecia.

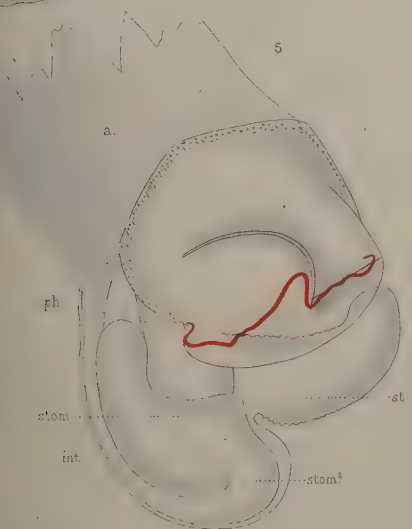
[*Figs. 1, 2 and 10, drawn by* Mr. E. Wilson, *are of the natural size. The remaining figures were drawn with* Zeiss, *A Obj. and have not been reduced*].

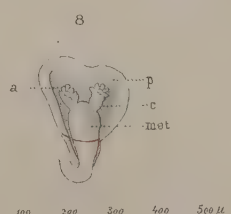












S. F. Harmer del.

P. W. M. Trap impr.

PLATE II.

Structure of the coenoecium.

Figs. 11—13. — *Cephalodiscus levinseni.*
Figs. 14—16. — *C. gracilis.*
Figs. 17, 18. — *C. sibogae.*
Figs. 20, 21. — *C. dodecalophus.*
Fig. 19. — *Rhabdopleura normani.*

Fig. 11. *C. levinseni.* — Part of the coenoecium (GREENOUGH's binocular, a^0). The diameter $AB = 12$ mm.; the length of the peristome $B = 4{,}2$ mm.: — *z.*, zooids, each contained in a distinct compartment ("zooecium") of the coenoecium; the varying positions of the pigment-line indicate a considerable variety of position in the proboscis; *o.*, orifice; *pst.*, peristome; *e.*, embryos.

Fig. 12. *C. levinseni.* — The peristome marked *A* in fig. 11, to shew the laminated structure of the coenoecium (GREENOUGH, a^3). For explanation of *a*, *b*, see text (p. 9); *c*, a secondary lamella.

Fig. 13. *C. levinseni.* — Two young peristomes (GREENOUGH, a^3).

Fig. 14. *C. gracilis.* — The peristomial filament marked *B* in fig. 15 (GREENOUGH, a^3).

Fig. 15. *C. gracilis.* — Portion of a colony, shewing the continuous cavity of the coenoecium (GREENOUGH a^0): — *z.*, masses of zooids, which are so crowded that their limits are not easily seen; *b.*, bud; *e.*, embryos; *o.*, orifices; *a.*, an occluded orifice; *fil.*, peristomial filaments of coenoecium, surrounding orifices; *B*, the filament shewn in fig. 14.

Fig. 16. *C. gracilis.* — End of another branch, more highly magnified than fig. 15 (GREENOUGH, a^2): — *a.*, *b.* orifices. (For explanation of *c*—*f*, see text, pp. 12, 13).

Fig. 17. — *C. sibogae.* — End of a branch of the coenoecium (GREENOUGH, a^2): — *e.*, *f.*, *i.*, orifices. (For explanation of other letters, see text, pp. 14, 15).

Fig. 18. *C. sibogae.* An erect branch of the coenoecium, less highly magnified (GREENOUGH, a^0). The position of the orifices is indicated by the peristomial filaments (*fil.*). The dark patches are foreign inclusions: — *B.*, part of the encrusting base of the coenoecium.

Fig. 19. *Rhabdopleura normani.* — Free end of a peristome (ZEISS, C). (For explanation of lettering, see text, p. 8).

Fig. 20. *C. dodecalophus.* — Portion of coenoecium (GREENOUGH, a^3).

Fig. 21. *C. dodecalophus.* — Portion of coenoecium, less highly magnified (GREENOUGH, a^0): — *b*, *c*, orifices. (For explanation of other letters, see text, p. 16).

[*The figures on this Plate were drawn as follows:*

GREENOUGH's *binocular*, a^0: — Figs. 11, 15, 18, 21.
GREENOUGH's *binocular*, a^2: — Figs. 16, 17.
GREENOUGH's *binocular*, a^3: — Figs. 12, 13, 14, 20.
ZEISS, C: — Fig. 19.

All the figures were afterwards reduced $^1/_2$, *or two diameters*].

S. F. Harmer del.

P. W. M. Trap impr.

PLATE III.

Figs. 22, 25—32. — *C. gracilis.* Figs. 23, 24. — *C. levinseni.*

Fig. 22. *C. gracilis.* — View of a reconstruction, made by the ground glass method, with the assistance of a plasticine reconstruction, from the specimen shewn in Pl. V, figs. 43—53. The details of the first arm (*R. 1*) are based on the individual shewn in Pl. I, fig. 7. The lateral flexure of the specimen indicated by figs. 45—53 has for the most part been omitted. The left ovary (*ov. l.*) is mainly occupied by a single large ovum. The broad pharynx (*ph.*) is seen from its narrow edge, the sharp bend just before its junction with the oesophagus (*oes.*) being probably the result of muscular contraction, which has also affected the dorsal vessel (*d. v.*). The last four arms (*R. 2—5*) have been cut off near their bases, which in the case of *R. 3—5* pass transversely outwards, while *R. 5* is rotated round its own longitudinal axis so much that its groove faces posteriorly.

Fig. 23. *C. levinseni.* — A reconstruction similarly made by the ground glass method; seen from the posterior surface and somewhat from the left. The proboscis (*p.*) is directed forwards, shewing the long, narrow proboscis-stalk (*prob. st.*) characteristic of this species; its morphologically anterior epithelium is infolded in a complex manner. There is also some rotation of the proboscis-stalk round its principal axis, since the left proboscis-pore (*p. p. l.*) lies at the edge of the drawing, while the right pore (*p. p. r.*) is also brought to the left of the median plane of the metasome. The right arms are already separate from one another, but *R. 2* turns ventrally from its origin, and is not visible in this view. On the left side, the section passes at a more ventral level, so that the common arm-base (*a. b.*) is seen, continuous with the left lobe of the operculum (*op.*). The region of the central nervous system (*c. n. s.*) is convex, and through it is seen the notochord (*nch.*). The dorsal vessel (*d. v.*) lies in the dorsal mesentery (*d. m.*), and the left ovarian vessel (*ov. v.*) is also seen: — *r.* is a lobe of the rectum; *g. s.*, seen through the left ovary, is the projecting portion of the pharyngeal wall leading from its dorsal diverticulum to the external aperture (*g. s. e.*) of the slit.

Fig. 24. *C. levinseni.* — Anterior view, seen somewhat from the right side, of the same reconstruction, the details of the upper lip added from a plasticine reconstruction. The arms are omitted, with the exception of part of *R. 2*. In addition to the median ventral projection of the proboscis-stalk, the upper lip is traversed by two ridges on each side, thus giving rise to three oral grooves on each side of the middle line. The greater part of the ventral wall of the mouth is cut away, with the exception of a fragment of the lower lip, seen in the foreground, in the middle line. The convex dorsal wall of the pharynx (*ph.*) is exposed, on either side of which is one of the deep pleurochordal grooves; the right gill-slit (*g. s.*), cut near its external aperture, opens nearly vertically into one of these, and on its median side is seen the blind end of one of the anterior horns of the metasomatic cavity (*b. c.*^{3} *a.*). The right collar-canal has its external opening (*c. c. e.*) directed dorsally, while between this and the internal opening is the problematical tissue (*x.*) of the collar-canal, attached above to a fold of the body-wall of the collar. The free edge of the right lobe of the operculum (*op.*) is directed dorsally, that of the left lobe ventrally.

Fig. 25. *C. gracilis.* — Another view of the specimen shewn in fig. 22, from a plasticine reconstruction. The thickness of the layers of plasticine having been somewhat too great, the transverse diameter is exaggerated. The figure shews that both the operculum and the arms are modifications of the anterior free edge of the collar: — *g. s. r.* right gill-slit; *c. c. e.* external opening of right collar-canal; *g. s. l.* position of opening of left gill-slit; *b. w.*, body-wall of metasome.

Fig. 26. *C. gracilis.* — Base of stalk of fig. 7 (ZEISS, DD): *d.*, basal disc; *p.*, proboscis of bud.

Fig. 27. *C. gracilis.* — Base of stalk of a functional zooid, with a young bud (ZEISS, C). The collar of the the bud shews indications of the first pair of arms (*a.*); and both the first (*b. c.*^{1}) and second (*b. c.*^{2}) body-cavities are visible.

Fig. 28. *C. gracilis.* — Part of stalk of Fig. 29, shewing the two stalk-vessels (ZEISS, C).

Fig. 29. *C. gracilis.* — Posterior view of metasome of a bud, at about the stage of fig. 32, shewing the posterior vessel (*p. v.*) of the stalk ending on the alimentary canal, and the anterior vessel (*a. v.*) prolonged for a short distance along the anterior body-wall (ZEISS, C).

Fig. 30. *C. gracilis.* — Anterior view of a bud (ZEISS, C). The left half of the proboscis is injured, and the first arm of the same side has been lost. The mouth (*m.*) is seen through the proboscis; the arms possess terminal vesicles, and the bases of the posterior pair are continuous with the operculum (*op.*), the free edge of which is indicated by a circular line partly surrounding the mouth: — *al.*, developing alimentary canal.

Fig. 31. *C. gracilis.* — Advanced bud, seen from the left side (ZEISS, C), shewing the course of the food-grooves of the first three left arms (*L. 1—3*): — *p.*, edge of proboscis, which covers the greater part of the bud; *m.*, mouth, seen through the proboscis; *op. l.*, left lobe of operculum; *c. c. e.*, external aperture of left collar-canal; *g. s. e.*, external aperture of gill-slit; *ph.*, pharynx + oesophagus; *int.*, intestinal limb of alimentary canal.

Fig. 32. *C. gracilis.* — Posterior view of a similar bud (ZEISS, C): *c. n. s.*, position of central nervous system; *R. 1*, first right arm, thrown over to the left side; and, like *L. 2* and *L. 3*, possessing terminal vesicles; *m.*, mouth, seen through the rectum and pharynx.

[*Figs. 22—25 were drawn by* Mr E. WILSON. *All the figures were reduced* $^2/_3$].

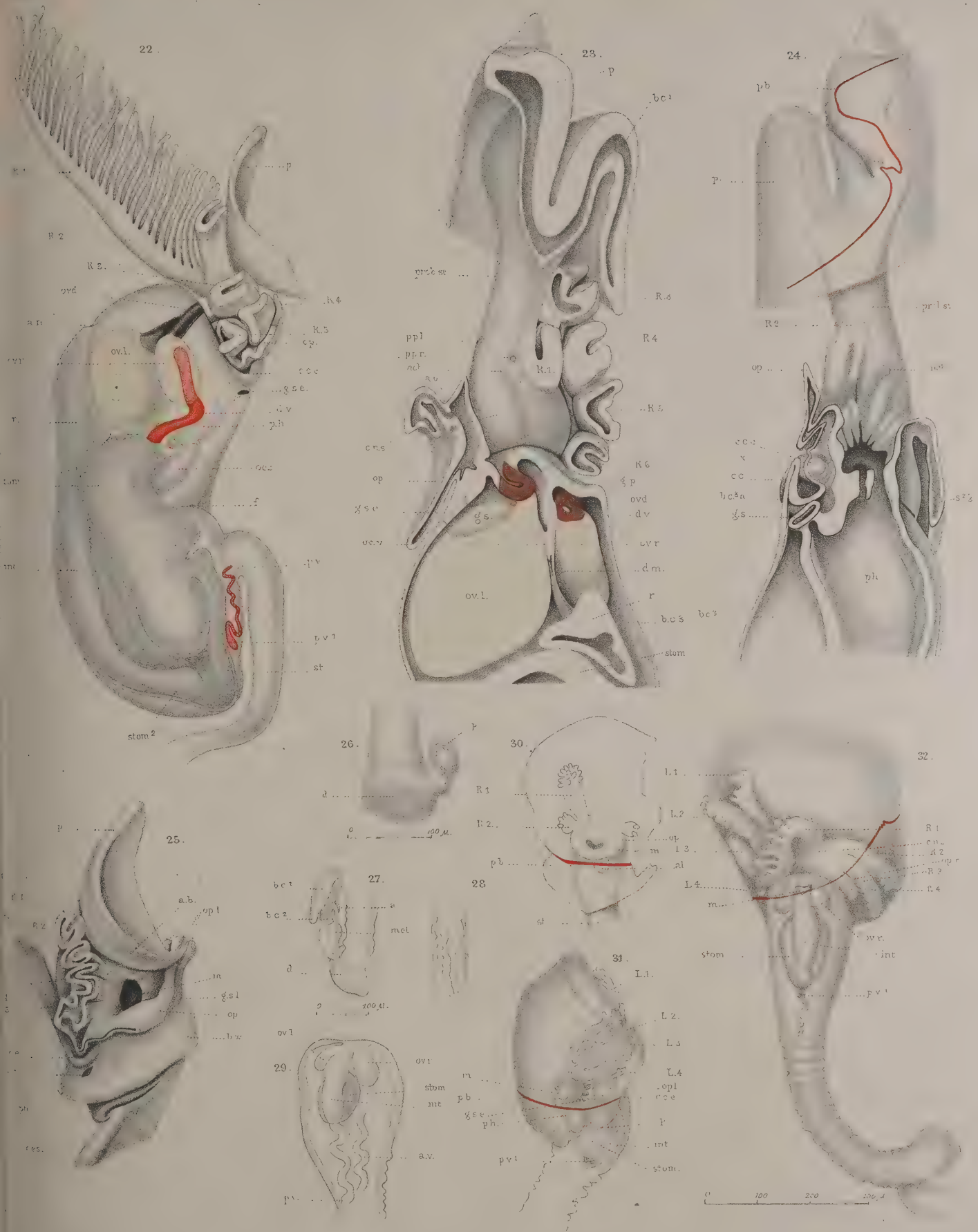


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PLATE IV.

Figs. 33—36. — *C. levinseni.*
Fig. 37. — *C. gracilis.*
Figs. 38—40. — *C. sibogae.*
Figs. 41, 42. — *C. dodecalophus.*

Fig. 33. *C. levinseni.* — Sagittal section of an old zooid, reconstructed from several sections. The proboscis (*p.*) is turned at right angles to the left of the specimen, so that its lateral parts are seen on the anterior and posterior sides. The first five arms of the left side (*L. 1—5*) are seen. The five unnumbered arms belong to the right side. The ovaries of this specimen are very small. The right ovary (*ov.*) with its pigmented duct, is represented, partially overlapped by the dorsal vessel (*d. v.*) and the rectum (*r.*).

Fig. 34. *C. levinseni.* — Median sagittal section of another zooid, drawn from a single section with the exception of part of the epithelium of the lower lip. The difference between this figure and fig. 33 is probably due to contraction of the longitudinal muscles. The anus (*an.*) is widely open, as a large mass of faeces is being discharged to the exterior. The course of the notochord (*nch.*) is indicated from the adjacent sections. The wall of the intestine is cut somewhat tangentially, so that one of its folds subdivides its lumen: the alimentary canal is not cut medianly at its principal bend. The proboscis (*p.*) has its normal position, but its stalk is greatly contracted, as indicated by the folds of its wall.

Fig. 35. *C. levinseni.* — A section to the right of the middle line of the same individual. A lobe (*op.*) of the operculum is seen disconnected from the basal part of the organ. The oral muscle (*or. m.*) is seen both dorsally and ventrally to the mouth (*m.*).

Fig. 36. *C. levinseni.* — A still more lateral section of the same individual: — *ms*, anterior longitudinal muscles of metasome, inserted into septum $^2/_3$; *c. c.*, edge of collar-canal; *g. s.*, wall of gill-slit; *p. p.*, internal opening of proboscis-pore.

Fig. 37. *C. gracilis.* — Median sagittal section, combined from the sections of a nearly sagittal series. The notochord is not well shewn in this individual.

Fig. 38. *C. sibogae.* — Median sagittal section of the alimentary canal of a neuter. The bend of the canal is injured, but its arrangement, as indicated by the neighbouring sections, is shewn by dotted lines.

Fig. 39. *C. sibogae.* — Part of a sagittal section of a neuter. The strongly marked epidermic thickening (*y*) behind the central nervous system (*c. n. s.*) is obviously ciliated, and probably has a nerve-layer at its base. The muscles are not indicated. Part of the hypopharyngeal groove is seen, and is marked *ph.* The upper lip is somewhat broken.

Fig. 40. *C. sibogae.* — Side view of an entire neuter individual. The anterior part of the zooid is lost, but the operculum (*op.*) is entire.

Fig. 41. *C. dodecalophus.* — Combined from three sections of the series to which fig. 42 belongs; to shew the relations of the muscles (*ms*) of the metasome to septum $^2/_3$, to the collar-canal (*c. c.*) which is cut tangentially, to the gill-slit (*g. s.*) and to the origin of the oral muscle (*or. m.*): — *p. p.* internal opening of proboscis-pore; *l. n.* origin of lateral nerve.

Fig. 42. *C. dodecalophus.* — Median sagittal section of the same specimen, drawn from a single section. The notochord is not cut medianly, but its opening into the pharyngeal diverticulum (*div.*) is seen in the middle of the glandular area in the anterior wall of that cavity.

[*All the figures were drawn with* ZEISS *C Obj., and were then reduced* $^1/_2$].

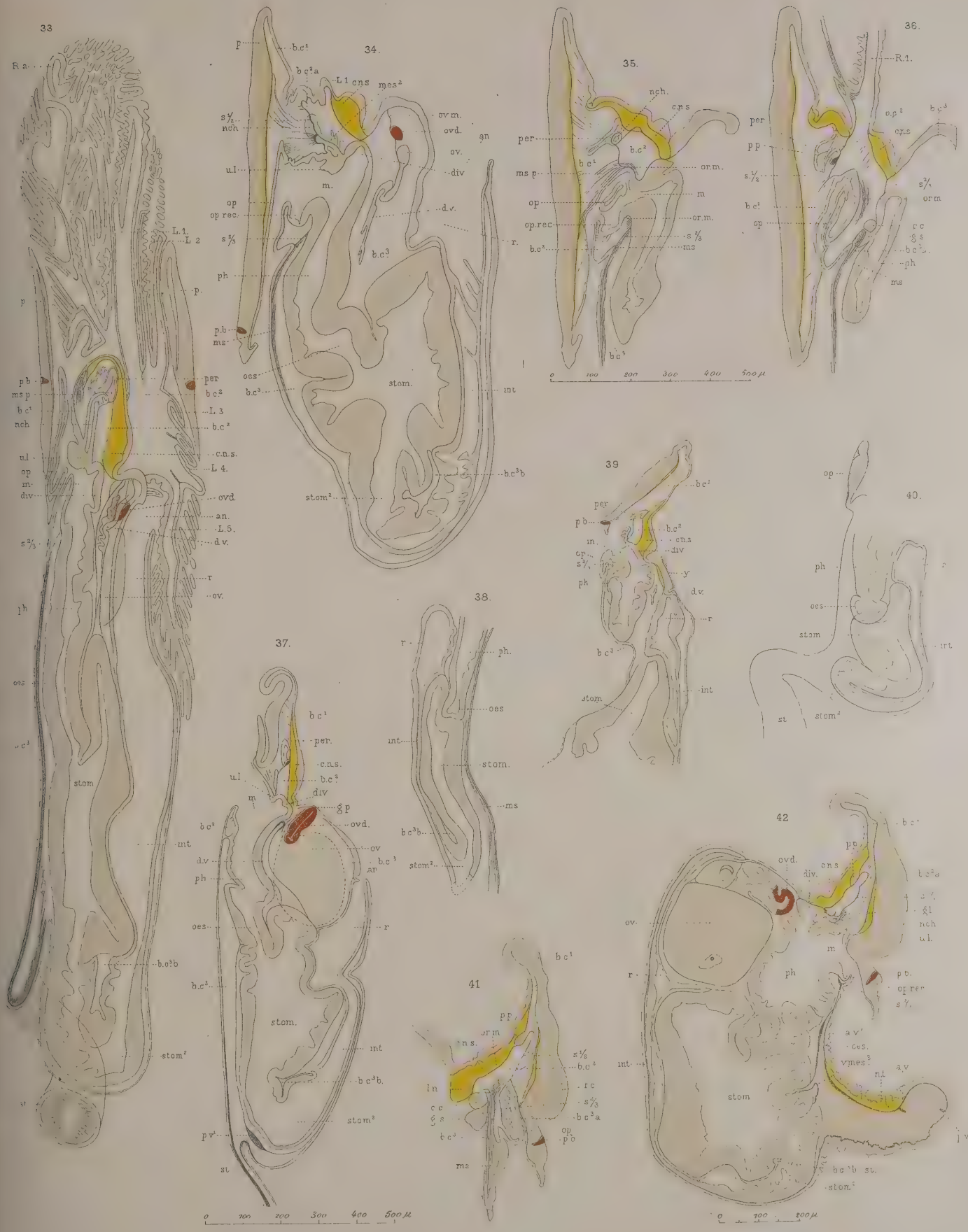

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PLATE V.

C. gracilis.

Figs. 43—53 (ZEISS, C) are obliquely sagittal sections of the specimen of which reconstructions are shewn in Pl. III, figs. 22, 25. The specimen had a strong lateral flexure towards the right, so that in figs. 50—53, the animal is cut in two separate pieces. It was abnormal in having a communication between the posterior side of the stomach and the intestine. The series starts with fig. 43 which is near the middle line, and proceeds outwards towards the right side of the body. Figs. 46—50 represent consecutive sections.

Fig. 43, near the median plane, cuts the mouth (*m.*), pharynx (*ph.*) and oesophagus (*oes.*) nearly medianly. The peritoneum (*pt.*) is loosely attached to the stomach, and does not enter the interval (probably in the main artificial) between the stomach and the intestine. The dorsal part of the collar-cavity (*b. c.*^{2}) is that of the left side, with the bases of the last three arms (*L. 3—5*). The stalk, which is cut at a bend, shews its anterior nerve-tract (*n. t.*): — *g. s.*, pleurochordal tissue of dorsal diverticulum of pharynx, continuous with the left gill-slit. The ovary (*ov. l.*) is that of the left side. The operculum (*op.*) is shorter than in the more lateral sections.

Fig. 44. — *f.*, end of the fold of the body-wall, which divides the sections shewn in figs. 50—53 into two parts; *ov. r.*, median edge of right ovary; *pl.*, pleurochordal tissue continuous with right gill-slit.

Fig. 45 passes just to the right of the mouth. The arms of the left side (*L. 1—3*) extend beyond the middle line of the collar to the right side of the animal; the base of the stalk (*st.*) is cut, and the opening of the second stomach (*stom.*^{2}) from the main stomach: — *b. c.*^{2}, right collar-cavity; *p. p.*, internal opening of right proboscis-pore; *r.*, right wall of rectum; *ov. v.* branch from dorsal vessel to left ovary; *g. s.*, wall of gill-slit.

Fig. 46. — The ventral half of the body, which is completely separated from the dorsal half by the fold of the body-wall (*f*) seen in fig. 45, is not represented: — *c. c. i.*, internal opening of right collar-canal; *g. s. e.*, external opening of gill-slit; *ovd.*, left oviduct, from which a discharge of pigment is taking place.

Fig. 47. — *p.*, proboscis, which has just separated from the collar; *R. 1, 2*, food-grooves of first and second right arms; *x.*, problematical tissue of collar-canal; *l. n.*., lateral nerve, originating from the central nervous system (*c. n. s.*); *ovd. r.*, pigment in epidermis indicating the median edge of the right oviduct.

Fig. 48. — *g. s.*, outer edge of gill-slit; *c. c. e.*, fold of epidermis into which the collar-canal opens in fig. 49.

Fig. 49. — *c. c. e.*, external opening of collar-canal; *x*, problematical tissue of collar-canal, extending to base of oral epidermis of operculum.

Fig. 50. — This and figs. 51—53 shew both parts of the metasome, the ventral half giving origin to the stalk (*st.*), and containing the second stomach.

Fig. 51. — The collar has just separated from the metasome, but a part of its free anterior edge still connects the base of the fifth arm (*R. 5*) with the operculum (*op.*): — *p. v.*^{1}, edge of termination of posterior stalk-vessel on the alimentary canal.

Fig. 52. — The operculum (*op.*) is no longer continuous with the last arm (*R. 5*). The stalk-vessels are not easy to distinguish from one another in the distal part of the stalk, but the zigzag vessel (*a. v.*?) there shewn is probably part of the anterior vessel.

Fig. 53. — The part of the body-cavity (*b. c.*^{3} *b.*) extending into the loop of the alimentary canal in figs. 50—52 is about to open into the general metasomatic cavity.

Fig. 54. — Longitudinal section of coenoecium through an orifice (*o.*): — *fil.*, peristomial filament (ZEISS, A).

Fig. 55. — Transverse section through the coenoecium (ZEISS, C).

Figs. 56—58. Frontal sections of a bud (transverse to its long axis) (ZEISS, F).

Fig. 56 passes a short distance dorsally to the point where the intestinal limb of the alimentary canal (*int.*) opens into the stomach (*stom.*). Both parts of the canal are contained in a common peritoneal investment (*pt.*).

Fig. 57 is taken more dorsally than the last. It shews the origin of the dorsal + ovarian vessels (*ov. v.*) from a reflection of the peritoneum of the alimentary canal.

Fig. 58 is the next section on the dorsal side of fig. 57. The two roots of the dorsal vessel (*d. v.*) have united, and the ovarian vessels (*ov. v.*) are being given off from the common trunk.

Fig. 59. — Frontal section of an older bud (ZEISS, F). The proboscis (*p.*) lies asymmetrically: — *c. c.*, right collar-canal, the emargination on the left side being merely the interval between the operculum (*op.*) and the metasome: *g. s.*, developing right gill-slit.

[*The figures have been reduced* $^1/_2$].

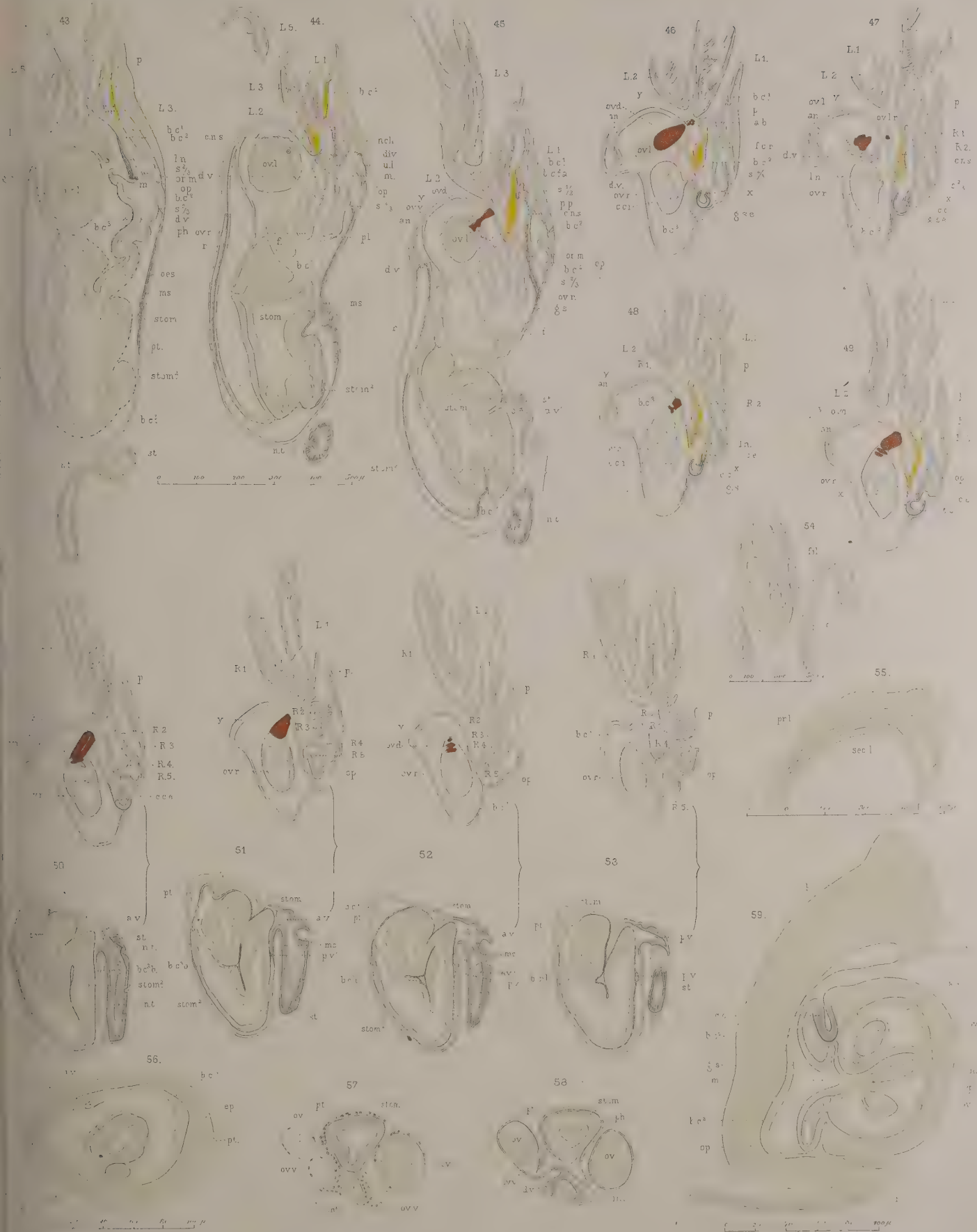

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PLATE VI.

C. gracilis.

Fig. 60. — Frontal section through arms and dorsal lobe of proboscis. All the arms appear in the section except the fourth left arm.

Fig. 61. — A more ventral section of the same specimen, cutting the dorsal edge of the metasome, with the two oviducts (*ovd.*). The grooves of the ten arms are indicated: — *op.r.*, right lateral lobe of operculum.

Figs. 62—70. — Frontal sections of another individual in which the ventral lobe of the proboscis is turned forwards, as in fig. 37. The arrangement of the arms and operculum was made out with the aid of a plasticine reconstruction.

Fig. 62. — Through the proboscis-stalk, in front of the beginning of the collar: — *per.*, pericardium, ventrally to which are seen the two principal groups of proboscis-muscles (*ms.p*).

Fig. 63. — Through the proboscis-stalk, in the region of the proboscis-pores (*p.p.*), and the tips of the anterior horns (*b.c.*^{2}*a.*) of the collar-cavities.

Fig. 64. — Through the notochord (*nch.*). The second left arm is directed ventrally from its base (somewhat as in the case of *R.1* in fig. 32), which is thus represented only by a part of the food-groove. The arm curves forwards later, so that it is cut near its tip in fig. 63 (*L.2*).

Fig. 65. — Through the mouth (*m.*) and the pharyngeal diverticulum (*div.*). The left half (*op.*) of the operculum is directed straight forwards (*i.e.*, away from the stalk), while the right half is folded backwards in a complicated manner, and thus does not appear in the section. The right arms, which are beginning to appear, are with the exception of *R.1* all thrown back along the posterior side of the metasome, while the left arms (seen in figs. 63, 64) are for the most part directed forwards. The ventral side of the right arm-base (*a.b.*) shews no trace of food-grooves.

Fig. 66. — Through the mouth (*m.*) which opens into the recess (*op.rec.*) formed by the base of the operculum. The part of the right lobe of the operculum marked *op'*. is backwardly directed, so that its oral surface faces posteriorly: — the direction of this lobe is probably correlated with that of the last arm, which is also thrown backwards; *a.b.*, ventral surface of right arm-base. The left collar-canal shews both its external (*c.c.e.*) and internal (*c.c.i.*) apertures. The fold of the body-wall between this and the left oviduct (*ovd.*) is of no special significance: — *x.*, problematical tissue of right collar-pore; *g.s.*, dorso-lateral grooves of pharynx leading from the dorsal diverticulum (*div.*) to the gill-slits.

Fig. 67. — Through the ventral wall of the left collar-canal (*c.c.*) and through the external opening (*c.c.e.*) of the right collar-canal. The opercular recess (*op. rec.*) is still present. The fold of the body-wall seen on the right side between it and the collar-canal appears from the reconstruction to be correlated with the throwing back of the arms and of the operculum of this side.

Fig. 68. — Through both gill-slits (*g.s.*) and the anterior horns of the metasomatic cavity (*b.c.*^{3}*a.*). The collar-cavities (*b.c.*^{2}) are here divided by a ventral mesentery (*v.mes.*^{2}).

Fig. 69. — Through the region of the pleurochords (*pl.*), on the aboral side of the gill-slits: — the muscles seen in *b.c.*^{3}*a.* in fig. 68 are continuous with those marked *ms.* in this figure.

Fig. 70. — Immediately on the dorsal side of the dorsal lobe of the stomach: — *ph.* is probably the posterior end of the pharynx (its passage into the oesophagus not being very obvious in sections cut in this plane).

Fig. 71. — Belonging to the individual shewn in figs. 60, 61, and cut in a frontal plane on the aboral side of the origin of the stalk: — *p.v.*^{1} termination of the posterior vessel (*p.v.*) of the stalk on the second stomach (*stom.*^{2}).

[*Fig. 71 was drawn with* ZEISS, *D D Obj. — The other figures were drawn with* ZEISS *C, and none of the drawings have been reduced*].

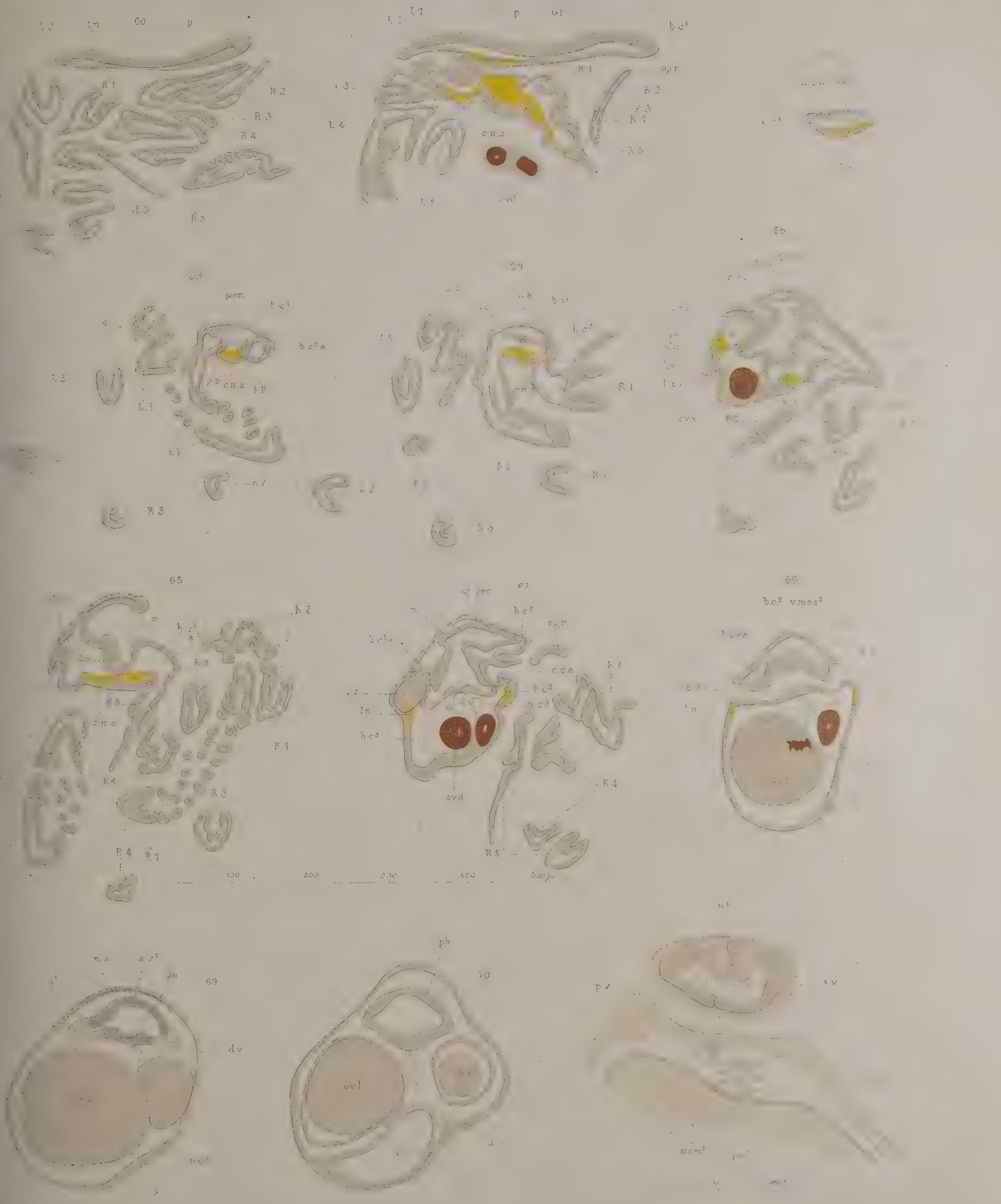

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PLATE VII.

C. sibogae.

Figs. 72—76, 79. — Male.
Figs. 77, 78. — Neuter.

Fig. 72. — Young male, posterior view. The left arm has been broken off, but its base is indicated by *L. a.* The refractive vesicles of which the epidermis of the arms of the male is almost entirely composed are not indicated in figs. 72—76, but they have the character shewn in Pl. IX, fig. 99: — *c. n. s.*, position of central nervous system.

Fig. 73. — Older male, shewing the right testis (*t. r.*). The left testis is smaller and is seen through the right arm (*R. a.*). The left arm (*L. a.*) is bifurcated at the tip. The arms are shorter than usual. The proboscis (*p.*) is a good deal folded.

Fig. 74. — Male, intermediate in age between figs. 72 and 73. The collar (*c.*) is marked off from the metasome (*met.*) by a conspicuous dorsal groove. The left side of the proboscis (*p.*) is somewhat injured. Both arms are incomplete distally.

Fig. 75. — Old male, seen obliquely from the right side. This specimen was cut into the sections represented in Pl. VIII, figs. 80—89. The right and left testes (*t. r.*, *t. l.*) are fully developed, and the metasome (*met.*) forms much the largest part of the animal. The arms (*R. a.*, *L. a.*) are shorter and thicker than in most of the young individuals.

Fig. 76. — Anterior view of old male, with longer arms. Some of the details of this specimen are further illustrated in Pl. IX, figs. 95, 96.

Figs. 77, 78. — Transverse sections of a neuter.

Fig. 77. — Through both apertures of the right collar-canal, and the external aperture (*g. s. e.*) of the right gill-slit. The muscular system is unusually strong in the neuters of *C. sibogae*: — *ms.* muscles of metasome, passing to septum $^2/_3$ (*s.* $^2/_3$); from the anterior side of this septum originate the oral muscles (*or. m.*), some of the fibres of which spread over the dorsal side of the mouth. The three epithelial ridges seen on the dorsal side of the pharynx pass in the section next in front of this one into a triangular upper lip which is of the same size as the three ridges together. The two grooves marked *m'*. pass laterally to the exterior, two sections on the ventral side of fig. 77; the mouth being thus situated at the level marked *m*. The operculum (*op.*) is directed forwards on the right side, and backwards on the left side.

Fig. 78. — A more posterior section of the same specimen. The gill-slit (*g. s.*) on the left side shews both its internal and external apertures. That on the right side is cut on the posterior or dorsal side of its external aperture; in the next section further back the deeply stained epithelial lobe between the two arrows has disappeared, and the vacuolated tissue of the gill-slit has become continuous with the extensively developed pleurochordal tissue of the dorso-lateral part of the pharynx. The whole of the arms of the right side are indicated (*R. 1—4*).

Fig. 79. — Obliquely sagittal section of an old male. The space between the central nervous system (*c. n. s.*) and its basement-membrane is probably an artefact. The collar is cut in a plane which is intermediate between sagittal and frontal: thus the projection *L. a.* is the base of the left arm, between which and the posterior wall of the proboscis is a groove (*f. c. l.*) corresponding with the principal food-channel of an ordinary *Cephalodiscus*; *f. c. r.* is the corresponding groove of the right side, and both grooves unite in the mouth, which occurs in a later section: — *R. a.* appears to be part of the right arm; while the arm cut transversely seems to be that of the left side; — *c. c.*, right collar-canal; *t. r.*, *t. l.*, right and left testes. The section does not involve more than half the length of the animal, which is bent into a *U*-form, in accordance with the shape of the coenoecial cavity in which it lies. The metasome and the testes are thus at least twice as long as the parts shewn.

[*Figs. 72—76 were drawn with* Zeiss *A Obj.; 77—79 with C Obj. None of the drawings have been reduced*].

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PLATE VIII.

C. sibogae.

Figs. 80—89. — Male.
Figs. 90—93. — Neuter.
Fig. 94. — Common stalk-base.

Figs. 80—89. — Frontal sections of the male shewn in Pl. VII, fig. 75. For explanation, see text, p. 86.
Fig. 80. — Through dorsal lobe of proboscis (*p.*). The arms (*L.a.*, *R.a.*) are somewhat macerated.
Fig. 81. — Through region of pericardium (7 sections later).
Fig. 82. — The next section.
Fig. 83. — The next section but one.
Fig. 84. — Through the mouth (3 sections later).
Fig. 85. — Two sections later.
Fig. 86. — Three sections later.
Fig. 87. — Three sections later.
Fig. 88. — Two sections later.
Fig. 89. — Forty four sections later.
Figs. 90, 91. — Frontal sections of a neuter.
Fig. 90. — Through the entire length of the right gill-slit (*g.s.*): — *pl.*, pleurochordal tissue of groove continuous with the left gill-slit and the left pleurochord.
Fig. 91. — Five sections nearer the stalk, cutting both pleurochords (*pl.*).
Fig. 92. — Obliquely frontal section of another neuter, cutting the posterior end of the ventral side of the collar. The arms of this specimen are shewn in Pl. IX, fig. 97.
Fig. 93. — Obliquely frontal section of the anterior end of a neuter. The left arms have been broken off, a torn place in the section marked *L.a.* indicating part of their base. The section shews the strong muscles (*ms.*) of the metasome inserted into septum $^{2}/_{3}$, from which starts one of the origins of the large oral muscle (*or.m.*). The wall of the gill-slit (*g.s.*) is composed of pleurochordal tissue. The ventral epithelium of the collar-canal (*c.c.*) is strongly ciliated. The problematical tissue (*x.*) of the collar-canal has a distinct row of nuclei on its coelomic border, while a band of muscle passes from it across the collar-cavity to the basement-membrane of the epidermis.
Fig. 94. — Common-base of stalks, in vertical section.

[*Fig. 94 was drawn with* ZEISS *D D Obj.; 80—93 with C Obj. None of the drawings have been reduced*].

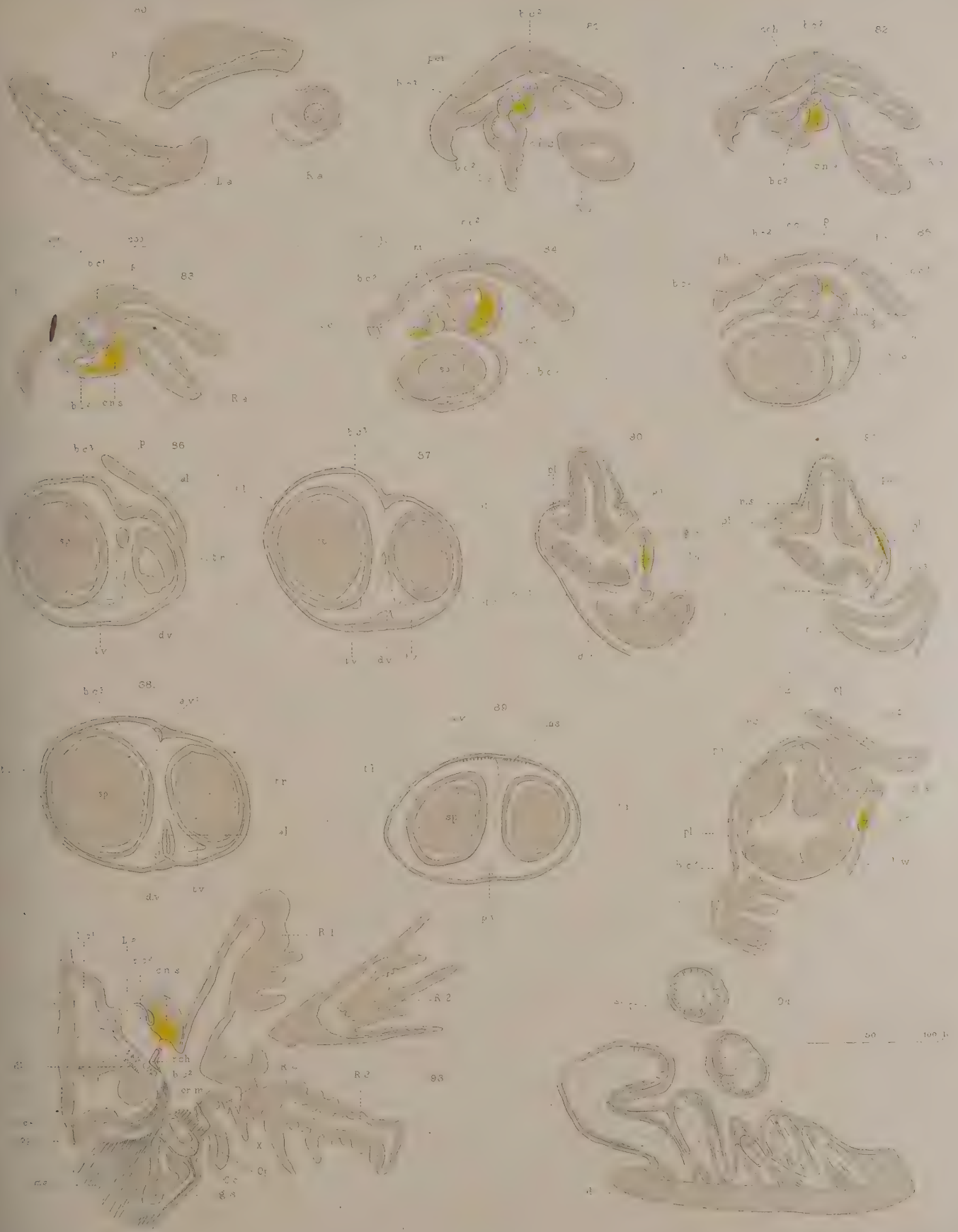

PLATE IX.

Figs. 95—99, 102, 103. — *C. sibogae.*
Figs. 100, 101, 104—110. — *C. levinseni.*

Fig. 95, 96. *C. sibogae.* — Two views (ZEISS, C) of the anterior part of the male shewn in Pl. VII, fig. 76.

Fig. 95. — Anterior view. The ventral lobe (*p'.*) of the proboscis is turned forwards, exposing the mouth (*m.*), on each side of which is seen a collar-canal (*c.c.*). The mouth leads to a vestigial alimentary canal, the intestinal limb of which is marked *r.* *R.a.* and *L.a.*, right and left arms; *t.r.*, *t.l.*, right and left testes.

Fig. 96. — Posterior view of the same specimen: — *c.n.s.*, swelling of collar due to the presence of the central nervous system; *g.p.* appears to be one of the generative pores; *d.v.*, dorsal vessel; *r.*, intestinal limb of alimentary canal.

Fig. 97. *C. sibogae.* — Frontal section of anterior end of the specimen shewn in Pl. VIII, fig. 92, shewing the proboscis (*p.*), and the four pairs of arms (ZEISS, C).

Fig. 98. *C. sibogae.* — Abnormal arm of a tentaculiferous individual, the distal end of which is produced into a long vesicle-bearing portion, resembling the arm of a male (ZEISS, C). The arm may belong to the first pair, but this is uncertain. The individual to which this arm belongs appears to have a pair of testes, in the position of the ovaries of a female *Cephalodiscus*. The testes, though small, seem to be functional. The specimen in other respects resembles a normal neuter: — *tent.*, tentacles.

Fig. 99. *C. sibogae.* — Base of arm of a young male, partly in optical section, shewing the characteristic epidermic vesicles, which do not occur in the proximal region of the arm (ZEISS, D D).

Fig. 100. *C. levinseni.* — Obliquely sagittal section of a young individual (ZEISS, C). The proboscis-stalk is strongly contracted and bent, as is indicated by the fold (*f.*) of its dorsal body-wall: — $a.^1$, one of the first arms.

Fig. 101. *C. levinseni.* — Lateral sagittal section of an old individual with reversed proboscis (ZEISS, C): — *f.*, *f.*, folds of body-wall of proboscis which appear to indicate the region where the rotation has been effected.

Fig. 102. *C. sibogae.* — Section of part of the basal encrustation of the coenoecium (GREENOUGH binocular, a^2.). The letters indicate the corresponding parts in fig. 103.

Fig. 103. *C. sibogae.* — Part of fig. 102, more highly magnified (ZEISS, A). For explanation of lettering, see text, p. 15; *g*, a secondary lamella.

Figs. 104—106. *C. levinseni.* — Sagittal sections of an embryo (ZEISS, C).

Fig. 104. — Lateral section, shewing the dorsal vacuolated ectoderm (*vac.*), the ventral thickening (*v. t.*) and the three body-cavities ($b. c.^{1-3}$).

Fig. 105. — Nearer the middle line: — the yolk-mass (*yk*) is divided into three portions.

Fig. 106. — More median region: — *s.o.*, sense-organ (?), which appears as an invagination of the vacuolated ectoderm (*vac.*). The two principal divisions of the yolk-mass are less clearly seen here than in some of the figures on Pl. XIV: *an.* is probably the future anus: $b.c.^2$ is visible on the dorsal side of the yolk-mass.

Fig. 107. *C. levinseni.* — Transverse section through the ventral border of the collar and part of the metasome (ZEISS, D D). The operculum (*op.*) is directed forwards, and appears emarginate in the middle line: — $v.mes.^2$, ventral mesentery of collar; $v.mes.^3$. of metasome; $s.^2/_3$, trunco-collar septum; *m.*, level of mouth; *b.m.*, basement-membrane of oral epidermis of operculum, with muscles.

Fig. 108. *C. levinseni.* — Transverse section of a peristome (ZEISS, A): — *m.r.*, mid-rib; *pr.l.*, primary lamellae.

Fig. 109. *C. levinseni.* — Transverse section through an entire branch of the coenoecium (GREENOUGH binocular, $a.^2$). The letters indicate the corresponding parts in fig. 110.

Fig. 110. *C. levinseni.* — Part of fig. 109, more highly magnified (ZEISS, A): *d*, *e*, *f*, cavities of zooecia; *pr. l.*, primary lamellae. For other letters, see text, p. 10.

[*All the figures have been reduced* $^2/_3$].

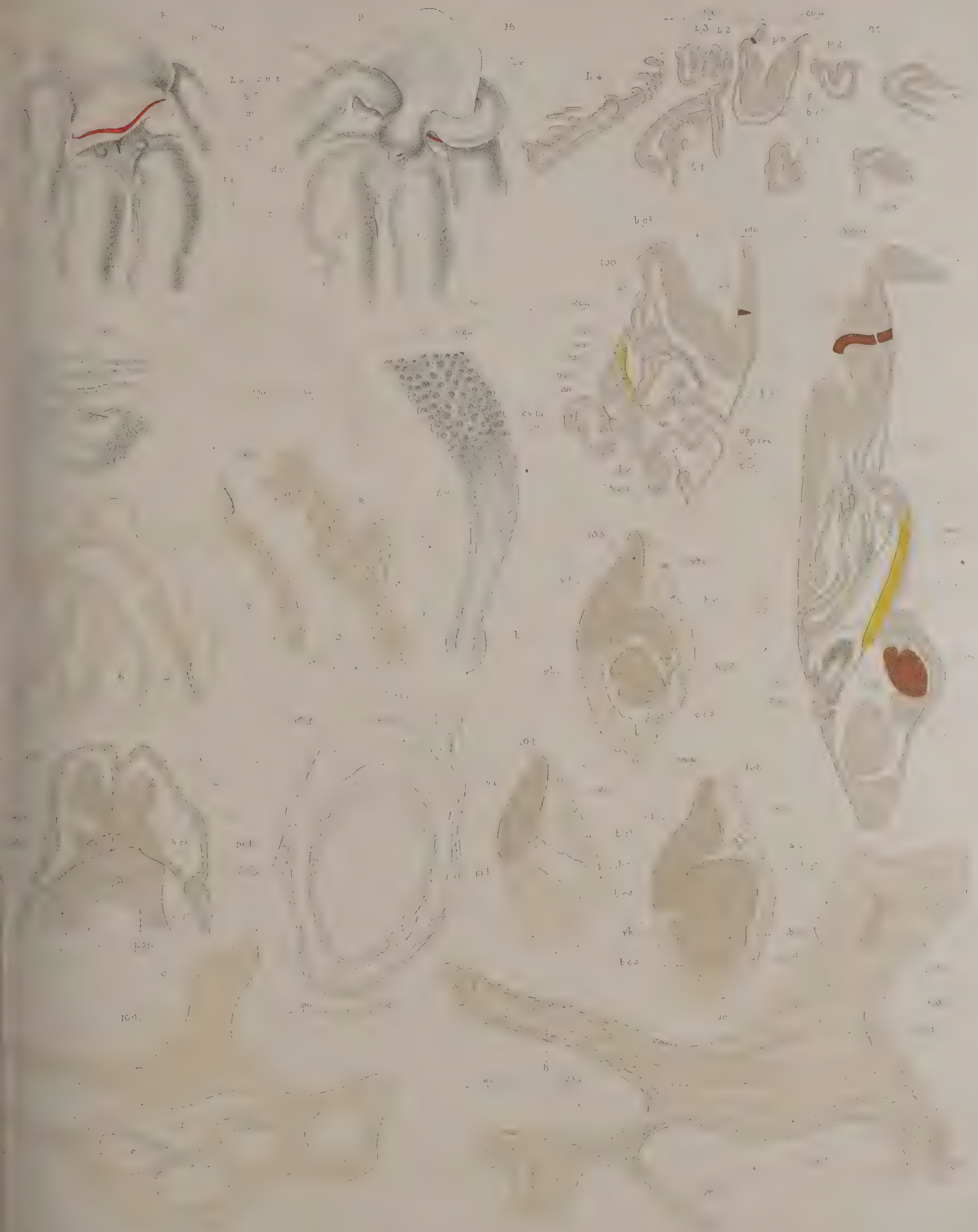

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PLATE X.

C. levinseni.

Figs. 111—125 are from a frontal series of an adult zooid. The proboscis is in the normal position.

Fig. 111. — Through dorsal lobe of proboscis, which is here strongly infolded (cf. Pl. III, fig. 24).

Fig. 112. — Thirty four sections further. Through pericardium (*per.*), both proboscis-pores (*p.p.*), and anterior dorsal horns of the collar-cavities (*b.c.*^{2}*a.*). The oval line surrounding the figure indicates the outline of the lumen of the coenoecial tube.

Fig. 113. — Six sections further. Through the anterior end of the notochord (*nch.*), the lumen of which is here specially large. The ventral lobe of the proboscis (*p.*) is about to separate from the proboscis-stalk.

Fig. 114. — Four sections further. The ventral lobe of the proboscis has just separated from the proboscis-stalk.

Fig. 115. — Seven sections further. Slightly dorsal to the mouth, through the transverse part of the pigment-band (*p.b.*) of the proboscis: — *prob.st.*, lobe of proboscis-stalk, cut separately; *p.*, fold of ventral lobe of proboscis.

Fig. 116. — Four sections further. Through the upper lip, which shews a distinct labial or oral groove (*l.g.*) on each side of its median ridge. The ventral lobe (*p.*) of the proboscis is folded in a complicated manner. The free edge of the left lobe (*op.l.*) of the operculum has appeared.

Fig. 117. — Two sections further, still through the upper lip, with its oral grooves (*l.g.*). The course of the food-groove of the fifth right arm (*R.5*) round the ventral side of the arm-base is illustrated by figs. 115—117, and shews the manner in which the grooves of the posteriorly directed arms pass towards the mouth.

Fig. 118. — Three sections further. Through the anterior wall (*div.*) of the pharyngeal diverticulum, and the beginning of the metasome (*met.*): — *b.m.* ridge of basement-membrane in right collar-cavity, indicating the base of the operculum.

Fig. 119. — Four sections further. Through the mouth (*m.*) and pharyngeal diverticulum (*div.*). The mouth opens straight forwards, as in Pl. IV, fig. 33. The left half of the operculum (*op.l.*) is folded, and lies principally in the plane of the section. The right lobe (*op.r.*) has its free edge directed towards the stalk, so that this lobe appears in the sections as far as fig. 123. The median part of the operculum and the base of both of its lateral lobes is, however, turned away from the stalk, so as to constitute the epidermic recess seen in figs. 121—123 (cf. Pl. IV, fig. 34): — *b.m.*, two ridges of basement-membrane indicating the base of the left lobe of the operculum.

Fig. 120. — Two sections further. The dorsal wall of the pharynx is beginning to be distinctly trilobed. This condition, which is more marked in fig. 121, indicates the commencement of the dorso-lateral grooves (*g.s.*) which lead to the gill-slits and pleurochordal grooves. The emargination in the dorsal body-wall of the metasome is a short longitudinal groove between the regions of the two oviducts, and may have something to do with directing the faeces when they escape from the anus.

Fig. 121. — Two sections further. Part of the thin dorsal wall of the right collar canal is cut: *or.s.* is possibly a vascular sinus.

Fig. 122. — Three sections further. The mouth (*m.*) opens into the epidermic recess (*op.rec.*) constituted by the base of the operculum. The median dorsal groove of the pharynx seen in the previous sections has died away.

Fig. 123. — Six sections further; through the ventral end of the mouth and both gill-slits. The rectum (*r.*) has appeared.

Fig. 124. — Five sections further. The distinction between the ordinary pharyngeal epithelium and the pleurochordal tissue is much less marked than in *C. dodecalophus*. The anterior horns of the third body-cavity are opening into the main cavity, of which a lobe divided by the ventral mesentery (*v.mes.*^{3}) appears between the pharynx and the collar-cavity: — *g.s.*, basement-membrane of ventral (posterior) wall of right gill-slit; *ov.v.*, ventral edge of ovarian vessel.

Fig. 125. — Thirteen sections further. The pleurochordal tissue has almost disappeared. The nerve-layer has become very indistinct, and is not represented.

[*The figures were all drawn with* ZEISS, *C Obj., and reduced* $^2/_3$].

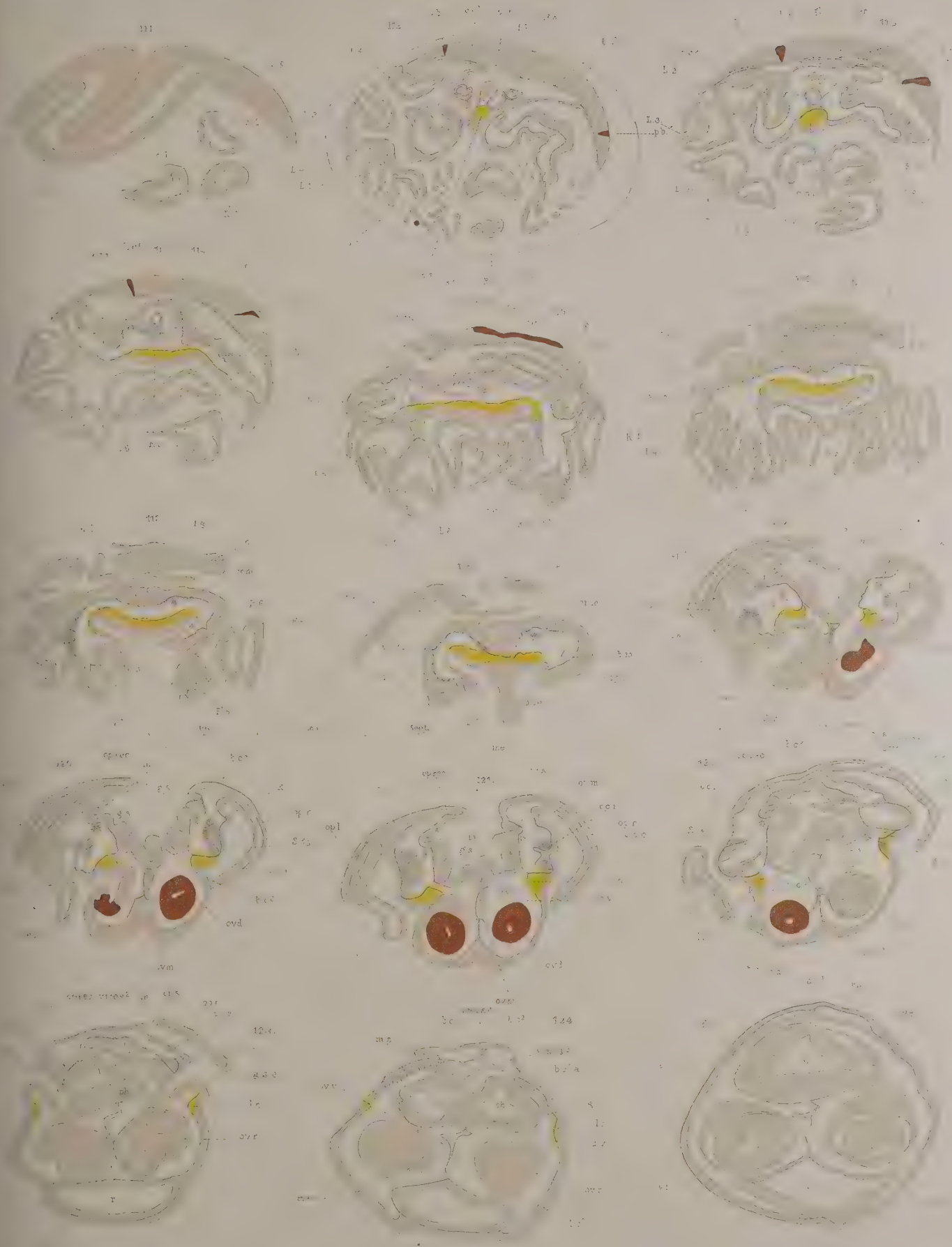

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PLATE XI.

Figs. 126—132, 137—140. — *C. levinseni.*
Fig. 133. — *C. dodecalophus.*
Figs. 134, 135. — *C. gracilis.*
Fig. 136. — *C. sibogae.*

Figs. 126—128, 132, 130 are continuations of the series *(C. levinseni)* shewn on Pl. X.

Fig. 126. — Twenty two sections further than fig. 125. — Through the oesophagus (*oes.*) The muscular layer is thicker and narrower, indicating the approach of the stalk. The nerve-layer (*n.t.*) is more definite. [The oesophagus terminates in the sixth section after fig. 126].

Fig. 127. — Fourteen sections further. Through the beginning of the stalk (*st.*).

Fig. 128. — Five sections further. The stalk (*st.*) is more distinct.

Fig. 129. *C. levinseni.* — Frontal section of a young individual, shewing the position of the stalk (*st.*), which is arranged as in Pl. I, fig. 5: — *g.s.r.*, ventral (posterior) wall of right gill-slit; *g.s.l.*, left gill-slit; *ph.*, folds of anterior (ventral) wall of pharynx; *c.c.*, ventral wall of left collar-canal.

Fig. 130. *C. levinseni.* — Seventeen sections further than fig. 132. Shewing the extension (*b.c.*^{3}*b.*) of the third body-cavity between the first (*stom.*) and second (*stom.*^{2}) stomachs.

Fig. 131. *C. levinseni.* — Obliquely transverse section of another individual: — *f.c.r.*, right food-channel between arm-base (*a.b.*) and right lobe of operculum (*op.r.*). The ventral epithelium and basement-membrane (*b.m.*) of this part of the collar are cut tangentially, so that the right collar-cavity appears to be divided into two halves. The arrow indicates the course of the food to the mouth.

Fig. 132. *C. levinseni.* — Four sections further than fig. 128. The stalk, which is more highly magnified than that of fig. 128, is now completely separate from the body.

Fig. 133. *C. dodecalophus.* — Section of stalk, transverse to its principal axis. The epidermis is folded; the nerve-layer has three principal concentrations, on the anterior side (*n.t.*), but appears to extend the whole way round the section.

Fig. 134. *C. gracilis.* — Similar section of the stalk of the individual shewn in Pl. VI, figs. 60, 61, cut near its junction with the body.

Fig. 135. *C. gracilis.* — Section of another stalk.

Fig. 136. *C. sibogae.* — Section of a stalk.

Figs. 137, 138. *C. levinseni.* — Two frontal sections of a young individual.

Fig. 137. — Through the dorsal part of the collar-cavities and the proboscis-pores (*p.p.*), which are seen to traverse the central nervous system (*c.n.s.*). The epidermis of the collar is injured on the left side.

Fig. 138. — Two sections nearer the ventral side, through the pericardium (*per.*), the internal openings of the proboscis-pores (*p.p.*), the notochord (*nch.*), and the anterior horns (*b.c.*^{2}*a.*) of the collar-cavities.

Fig. 139. *C. levinseni.* — Sagittal section of anterior end of an individual with reversed proboscis: *p.b.*, pigment-band of proboscis; *b.c.*^{2}*a.*, tip of anterior horn of the collar-cavity of the opposite side; *f.*, fold of wall of proboscis-stalk indicating the region where most of the twisting has probably taken place.

Fig. 140. *C. levinseni.* — Section through the left side of the individual shewn in Pl. IV, figs. 34—36: — *ph.*, tangential section of left edge of pharynx; *g.s.*, gill-slit; *c.c.*, collar-canal, in dilated condition. The second arm (*L.2*) is cut along its groove. The fourth and fifth arms appear, in other sections, in the positions indicated by *L.4*, *L.5*.

[*Figs. 132—136 were drawn with* ZEISS, *D D Obj., the others with C Obj. All are reduced* $^2/_3$].

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PLATE XII.

Figs. 141—157. — *C. dodecalophus.* Figs. 158—160. — *C. levinseni.*

Figs. 141—151. *C. dodecalophus.* — Obliquely sagittal sections, through the right half of the anterior end. Every second section is drawn, beginning with fig. 141, which is the most external. Fig. 151 is more highly magnified than the others. The series illustrates the relation of the arms and of the operculum to the rest of the collar, together with the more important parts of the nervous system. The muscles, and the filaments traversing the collar-cavity are only partially represented.

Fig. 141. — Shews the lateral part of the dorsal lobe of the proboscis (*p.*) and the six arms (*1—6*) of the right side. The longitudinal muscles are shewn in *5* and *6* only.

Fig. 142. — The lateral lobe of the operculum (*op.r.*) is cut tangentially. Arm *1* is still distinct, but *2—5* have passed into the common arm-base.

Fig. 143. — The ventral lobe of the proboscis is beginning to appear, with the end of the pigment-band. The arm-base is traversed by food-grooves, continuous with those of the arms. Grooves *3—6* are passing transversely inwards. The collar-cavity in the arm-base is interrupted by projections of the basement-membrane which are the first indications of the separation of the arms from the common base.

Fig. 144. — The first arm has joined the arm-base. The dorsal sides of the arms are marked *R. 1—6*; and the grooves *1—6*. Grooves *3—5* are shallower than in the last figure. The coelom of the part of the arm-base corresponding with arms *3—6* has become continuous. A fold of the dorsal wall of the proboscis is cut tangentially, and the nerve-layer is accordingly thicker here than in other parts of the section.

Fig. 145. — Grooves *4, 5* have quite disappeared, the anterior surface of the arm-base (*a.b.*) being here smooth.

Fig. 146. — The dorsal portion of the collar is beginning to be connected with the proboscis. The tip of the right anterior horn of the collar-cavity is seen projecting into the proboscis-cavity.

Fig. 147. — The first arm (*R. 1*) is cut at its base, its cavity communicating with the anterior horn of the collar-cavity. The two parts of the collar are about to become continuous: — *p.p.r.*, external aperture of right proboscis-pore.

Fig. 148. — A lobe of the operculum (*op.r.*) which is continuous with the base of the sixth arm, projects backwards, in the plane of the section, over the collar-pore, which is seen in fig. 151 (*c.c.e.*). The septum on the dorsal side of *op.r.* is a ridge of basement-membrane, indicating the point at which the operculum becomes free from the rest of the collar (cf. figs. 152, 153): — *p.p.r.*, right proboscis-pore, cut tangentially; *per.*, pericardium.

Fig. 149. — Cuts the animal at the level where the collar first joins the body: — *ovd.*, right oviduct, with the ovarian vessel (*ov.v.*) and mesentery (*ov.m.*); *mes.*^{3}, dorsal mesentery, on the other side of which is seen the left ovary (*ov.l.*) and the left lateral edge of the rectum (*r.*).

Fig. 150 shews the origin of the lateral nerve (*l.n.*) from the central nervous system (*c.n.s.*): — *div.*, edge of the pharyngeal diverticulum; *ovd.*, right oviduct; *p.p.l.*, internal opening of left proboscis-pore; *b.c.*^{2}*a.*, tip of anterior horn of left collar-cavity.

Fig. 151 cuts the tip of the notochord (*nch.*), which is supported by the dorsal mesentery of the collar; *p.p.l.*, external opening of left proboscis-pore; *c.n.s.*, ganglion-cells of central nervous system; *ov.l.* and *ov.r.*, left and right ovaries, with their respective mesenteries (*ov.m.l.*, *ov.m.r.*); *l.n.*, lateral nerve; *c.c.e.*, external aperture of right collar-pore, with its problematical tissue (*x.*); *or.m.*, oral muscle.

Figs. 152—157. — Frontal sections of a young individual, passing from the dorsal side towards the ventral side. The figures illustrate the arrangement of the oral grooves, the dorsal diverticulum of the pharynx, the pleurochords, the gill-slits and other organs.

Fig. 152, near the dorsal extremity of the pharyngeal diverticulum (*div.*), with its glandular patches, cuts the right lateral lobe (*op.r.*) of the operculum tangentially: — *gl.*, ventral end of glomerulus, attached to the anterior side of the notochord (*nch.*); *x.*, dorsal end of problematical tissue of right collar-pore, attached to the epidermic fold which separates the lateral lobe of the operculum from the rest of the collar; *g.p.*, right generative pore; *R. 4—6*, groove on the ventral surface of the common arm-base leading to the food-grooves of the 4th—6th right arms. The epithelial ridge (*e.r.*) seen in this figure and in figs. 153—155 is discussed on p. 62.

Fig. 153, through the left lateral lobe (*op.l.*) of the operculum, shews the dorsal ends of the pleurochords (*pl.*); *or.m.*, oral muscle.

Fig. 154. — The pleurochords (*pl.*) open into the diverticulum of the pharynx, on either side of its posterior groove. The right collar-canal (*c.c.r.*) lies in a direction which is seen to be at right angles to that of the corresponding gill-slit (*g.s.*, fig. 156).

Fig. 155, through the dorsal edge of the mouth, shews a labial or oral groove (*l.g.*) between the base of the operculum (*op.l.*) and a ridge (*e.r.*) which is prolonged dorsally as the epithelial ridge visible in figs. 154—152. The oral groove communicates with one of the anterior grooves of the pharyngeal diverticulum. The right pleurochordal region is about to open by the gill-slit, the dorsal wall (*g.s.*) of which is cut tangentially; *c.c.*, ventral wall of right collar-canal.

Fig. 156 shews both gill-slits (*g.s.*), the ventral wall of the left collar-canal (*c.c.*), and the anterior horns of the third body-cavity (*b.c.*^{3}*a.*), filled with longitudinal muscles. These structures just extend into fig. 155.

Fig. 157 shews that the pleurochords (*pl.*) extend back laterally along the pharynx. The operculum (*op.*) is about to terminate in the middle line, as is indicated by the absence of body-cavity in this region.

Figs. 158—160. — Diagrams of the proboscis and collar of *C. levinseni*, based on the specimen illustrated in Pl. X.

Fig. 158. — Diagrammatic posterior view of proboscis (*p.*), collar (*c.*) and dorsal part of metasome (*met.*); *p.p.*, proboscis-pores; *L. 1—6*, arms of the left side; *op.* operculum.

Fig. 159. — Diagrammatic anterior view of a specimen in which the proboscis-stalk is directed dorsally, and the buccal disc has been removed by a cut transverse to the proboscis-stalk. The operculum (*op.*) is supposed to have been stretched so as to pass completely outside the series of arms (cf. fig. 160): *L. 1—6*, food-grooves of the left arms; the body-cavity of the left arm-base is partially divided by ingrowths of the basement-membrane, corresponding with the intervals between the arms.

Fig. 160. — A similar diagrammatic view, with the proboscis in its usual position.

[*Figs. 141—150, 152—157 were drawn with* Zeiss, *C Obj., fig. 151 with* Zeiss, *D D. All the figures were reduced* $^1/_2$].

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PLATE XIII.

BUDDING.

Figs. 161—181. — *C. dodecalophus.*
Figs. 182—185. — *C. sibogae.*

Figs. 161—163. *C. dodecalophus.* — Consecutive sections through the base of an old stalk, transverse to its long axis, with a young bud (*b.*).

Fig. 164. — Sagittal section through base of an old stalk, shewing a very young bud ($b.^1$) and the base ($b.^2$) of the bud shewn in fig. 165.

Fig. 165. — More median sagittal section of $b.^2$ in fig. 164.

Figs. 166—172 are from an obliquely sagittal section of an old stalk, and are all drawn in the same relative position. Figs. 169, 172 shew the stalk, with its much wrinkled epidermis, and parts of the two buds $b.^1$, $b.^2$. The younger bud ($b.^1$) is further shewn in figs. 166—168; and the older one in figs. 170, 171.

Figs. 166—168 are frontal sections of the bud $b.^1$ in figs. 169, 172. Fig. 166 is through the proboscis; fig. 167 is through the proboscis and collar; and fig. 168 is through the metasome. Fig. 172 shews the metasomatic cavities passing through the epidermis of the parent-stalk.

Fig. 169. — Obliquely sagittal section of old stalk, with the two buds ($b.^1$, $b.^2$). The section of $b.^1$ is between fig. 168 and fig. 172: that of $b.^2$ is between fig. 170 and fig. 172.

Figs. 170, 171 are frontal sections of the bud $b.^2$ in figs. 169, 172. Fig. 170 is at the bend of the alimentary canal; fig. 171 is nearer the dorsal side: — *int.*, intestinal limb of alimentary canal.

Fig. 172 is through the edge of the basal sucker (*d.*) of the stalk, and it follows fig. 169.

Figs. 173, 174. — Two sagittal sections of a moderately old bud.

Figs. 175—177. — Three sagittal sections of a young bud, with part of the parent stalk.

Figs. 178—180. — Three obliquely sagittal sections of an older bud, which has just begun to develop its first pair of arms.

Fig. 181. — Median sagittal section of an advanced bud.

Figs. 182—185. *C. sibogae.* — Obliquely sagittal sections of an advanced neuter bud.

Fig. 182. — The pleurochordal groove (*pl.*), the histological characters of whose walls are not yet fully differentiated, appears to be separated from the rest of the pharyngeal cavity by one of the dorso-lateral epithelial ridges seen in Pl. VIII, figs. 90—92. In the sections before this one is reached, the right gill-slit communicates with the anterior end (*g.s.*) of this groove. The cells lining the pharyngeal diverticulum (*div.*) are much vacuolated: — $b.c.^2r.$, right collar-cavity.

Fig. 183. — Through the other dorsal half of the collar-cavity ($b.c.^2l.$): — *p.p.* internal opening of left proboscis-pore.

Fig. 184. — Passing to the left of the mouth, but shewing the right gonad-rudiment (*g.*).

Fig. 185. — Through the external opening of the left gill-slit (*g.s.e.*) and collar-canal (*c.c.e.*). The rectum (*r.*) already contains faeces. The beginning of the wall of the stomach (*st.*) is cut tangentially.

[*The figures were all drawn with* ZEISS, *DD Obj. and reduced* $^2/_3$].

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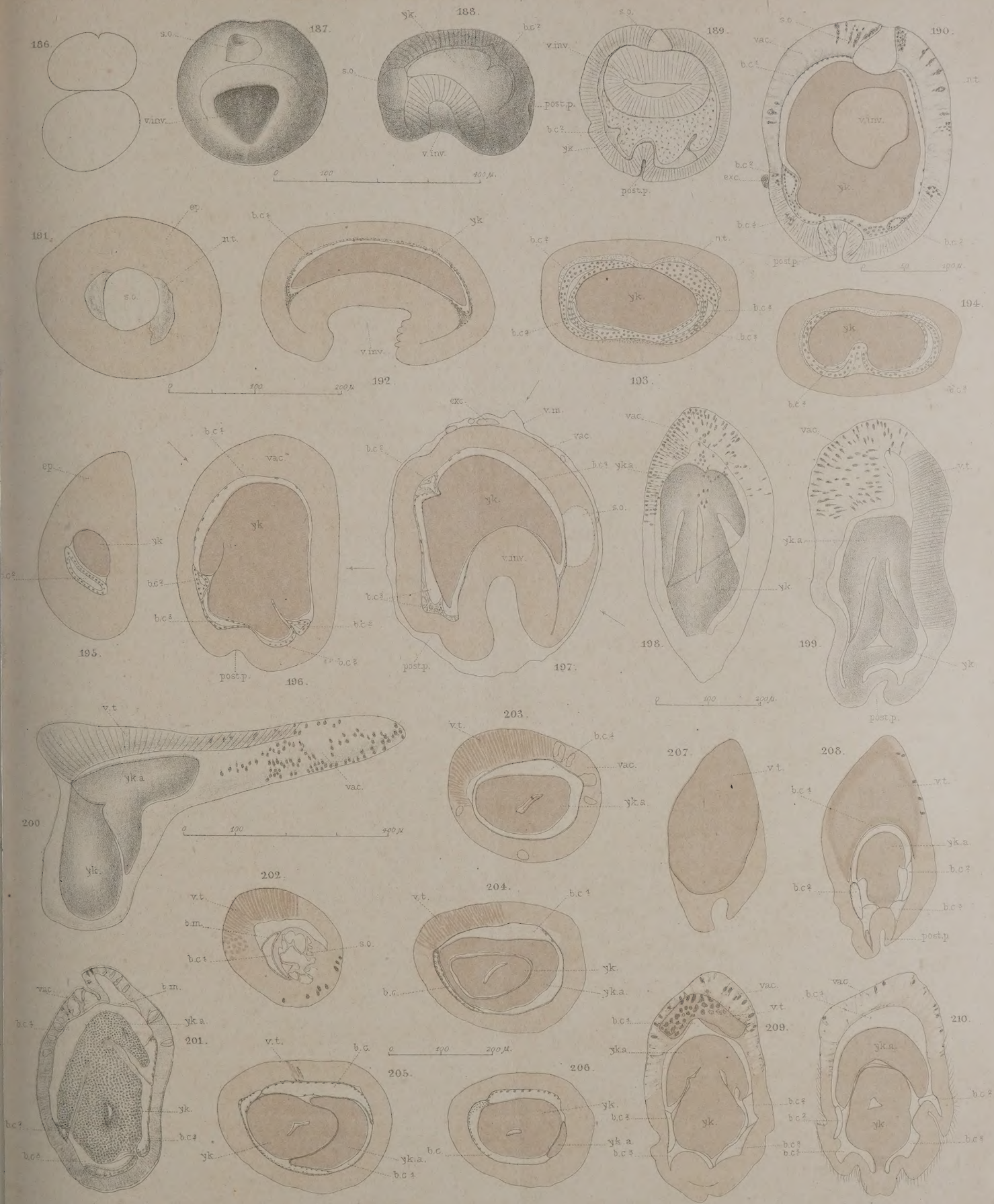
PLATE XIV.

EMBRYOS.

Figs. 186—197. — *C. gracilis.*
Figs. 198—210. — *C. levinseni.*

Fig. 186. *C. gracilis.* — Two cell stage, mounted whole.
Fig. 187. — Ventral view of an advanced embryo.
Fig. 188. — Lateral view of a similar embryo: — *b.c.*^{2}, position of collar-cavity.
Fig. 189. — Optical frontal section of a similar embryo from the ventral side. The constrictions at the sides of the yolk (*yk*) correspond with those in which the collar-cavities lie in other preparations; *v. inv.*, external aperture of the ventral invagination.
Fig. 190. — Actual frontal section, more highly magnified: — *v.inv.*, dorsal wall of ventral invagination, cut tangentially (other sections of the same embryo are shewn in figs. 195, 196).
Fig. 191—194. — Transverse sections of a similar embryo. Fig. 191 is through the anterior sense-organ (*s.o.*); fig. 192, through the anterior part of the ventral invagination (*v.inv.*); fig. 193, through the collar-cavities (*b.c.*^{2}) and the metasomatic cavities (*b.c.*^{3}); and fig. 194, through the metasomatic cavities (*b.c.*^{3}).
Figs. 195, 196. — Horizontal sections of the individual shewn in fig. 190.
Fig. 195 is through the dorsal region of the embryo: — *b.c.*^{2}, collar-cavity.
Fig. 196 is between fig. 195 and fig. 190: — *vac.*, vacuolated ectoderm, extending as far as the two arrows.
Fig. 197. — Nearly median sagittal section of a similar embryo. The region of the posterior pit (*post.p.* is, however, cut somewhat frontally, so that both third body-cavities (*b.c.*^{3}) are visible. The somewhat crumpled vitelline membrane (*v.m.*) is seen, while between it and the ectoderm are what are probably excretory granules (*exc.*). The anterior ectoderm between the two arrows has the vacuolated character shewn in fig. 190.
Figs. 198—210. *C. levinseni.*
Fig. 198. — Advanced embryo, seen obliquely from the dorsal side. The central yolk-mass (*yk*) has a lumen; the edge of the reflected part of the yolk is not easily seen where it crosses the central mass, but is probably correctly represented: — *vac.*, vacuolated ectoderm, which in the embryos of this species contains numerous refractive bodies.
Fig. 199. — Another embryo, probably somewhat older than fig. 198, seen from the side. The embryo was found in a peristome, close to its orifice, and may have been about to be liberated.
Fig. 200. — Advanced embryo of unusual appearance, in which the vacuolated ectoderm (*vac.*) and the ventral thickening (*v.t.*) have together the appearance of the proboscis of the adult.
Fig. 201. — Obliquely sagittal section of an advanced embryo. The vacuolated ectoderm (*vac.*) is invaginated dorsally and in front. It is uncertain whether the collar-cavity is seen on the ventral side, which is turned to the right. A space (artificial?), which is also seen in fig. 202, occurs outside the basement-membrane (*b.m.*) at the anterior end.
Figs. 202—206. — Five sections of a transverse series of a similar embryo. The limits between the second and third body-cavities are not obvious in this series.
Fig. 202. — Through the anterior end.
Fig. 203. — Through the anterior yolk-mass.
Fig. 204. — Through the central yolk-mass, which is here encircled by the reflected part of the anterior yolk.
Fig. 205. — Through the extreme posterior end of the ventral thickening.
Fig. 206. — Through the extreme posterior end of the anterior yolk-mass.
Fig. 207—210. — Four sections of a frontal series of an older embryo.
Fig. 207. — Through the entire area of the ventral thickening (*v.t.*).
Fig. 208. — Near the ventral surface, but cutting the five coelomic spaces.
Fig. 209. — Through about the middle of the embryo.
Fig. 210. — Through the dorsal half of the embryo.

[*Figs. 190—197 were drawn with* ZEISS, *D D Obj.; figs. 186—189 and 198—210 with* ZEISS, *C. All the figures were reduced* $^2/_3$].



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